Methods for Integrated Use of Fisheries Research Survey Information in Understanding Marine Fish Population Ecology and Better Management Advice

Improving Methods for Evaluation of Research Survey Information under consideration of Survey Fish Detection and Catch Efficiency

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Thesis

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Contents

In Section 1.3 the underlined referred publications are papers directly under the thesis. Additionally,there is made reference to relevant reference and supportive papers (not underlined) where the thesis author is also (co-)author and those papers are listed in a specific section in the list of publications.

Cover photo, R/V Dana: Line Reeh.

Chapter 1

General Introduction (Background, Objectives, Outline)

1.1 Background

Monitoring of changes in abundance of commercially important or ecological important marine fish stocks is essential for performing rational, effective and biological sustainable marine fisheries management and scientific management advice (e.g. Gulland 1988; Hilborn and Walters 1992; Godø 1994; Rijnsdorp et al. 1996; Simmonds and MacLennan 2005; Beddington et al. 2007). Management advice and associated fish and fisheries monitoring is a main pillar in the EU Common Fisheries Policy (CFP; EC 2002). The Ecosystem Approach to the Management of Human Activities (EAM; Rice et al. 2005), the Integrated Maritime Policy (IMP; EC 2007), and the Marine Strategy Framework Directive (MFSD; EC 2008a) have been adopted by the EU as the fundamental approaches to attaining marine and maritime sustainable development and has been integrated into a raft of conventions, agreements, etc., related to policies and best practices. Fishery management is necessary for ecological sustainable exploittation of the marine resources and to avoid collapse of important fish stocks such as previously observed for some of the world's major fish stocks, e.g. Norwegian spring spawning herring (*Clupea harengus)*, North Sea herring, Peruvian anchoveta (*Engraulis ringens*) and Chinese yellow croaker (*Larimichthys polyactis*) in the 1970'ies and Newfoundland northern cod (*Gadus morhua)* in the early 1990's with very long stock recovery periods after the collapses (Hilborn and Walters 1992; Hutchings 1996; He 2010). Accordingly, fishery resources are not "inexhaustible" (Hilborn and Walters 1992; Simmonds and MacLennan 2005; Beddington et al. 2007; He 2010), and the marine ecosystems are sensitive to fishing (Greenstreet et al. 1996; 1999; EU STECF 2012; Gascuel et al. 2014). Also fishery management is necessary to assure economic and sociological sustainable fishing sectors in many regions and local areas (Gulland 1988; Hilborn and Walters 1992; Jennings et al. 2001; Hilborn 2007). The EAM emphasizes that humans are integral components of ecosystems whereby human social and economic systems constantly interact with the physical, chemical and biological parts of the ecosystem (Rice et al. 2005).

Fisheries independent scientific surveys of marine stocks have central importance in scientific management advice as basis for fish single stock (and multi-species) assessments and forecasts (e.g. Hilborn and Walters 1992; Simmonds and MacLennan 2005; EC 2002; ICES 2013a;b;c;d;e) and for formulating sustainable management strategies for many fisheries throughout the world, e.g. from the international fishery advisory bodies such as ICES (International Council for Exploration of the Sea, www.ices.dk), NAFO (North-West Atlantic Fisheries Organization, www.nafo.org), ICCAT (International Commission for the Conservation of Atlantic Tunas, www.iccat.org), EU STECF (Scientific, Technical and Economic Committee for Fisheries https://stecf.jrc.ec.europa.eu/), and FAO (Food and Agricultural Organization of the United Nations, www.fao.org). Among other, the data are used in the 'tuning' of VPA and similar assessment methods (e.g. Gulland 1988; Jennings et al. 2001; Hilborn and Walters 1992; Nielsen and Berg 2014), and for non-exploited stocks this may be the only source of information available to determine densities and relative stock (or species) abundance (e.g. Daug et al. 2002). Especially fisheries (trawl, gillnet, trap, etc.) surveys and combined hydroacoustic and fisheries surveys are important in context of fisheries management and stock assessment (Simmonds et al. 1991; Hilborn and Walters 1992; Nielsen et al. 2001a; Simmonds and MacLennan 2005; ICES 2013d;e). Other types of surveys are eggs- and larvae-surveys for e.g. pelagic species and photographic surveys for e.g. shellfish (e.g. Jansen et al. 2012). A frequent criticism of research survey data is that the survey time series only contain relatively few observations with only limited coverage in time. In comparison, there will usually be a much higher number of observations from commercial fishery. However, fishery information is practically never based on a stratified random or systematic sampling design covering the full stock (all life stages,

ages and sizes) and the full stock distribution area, but rather target certain parts of the stock in certain areas and periods (e.g. Pennington and Strømme 1998). Fishery is typically subject to change in fishing power over time because of technical developments and increased fishermen skills (education, knowledge, etc). The reliability of fisheries dependent data and commercial CPUE (Catch Per Unit of Effort) series is reduced in stock assessment if fishing strategies or fishing efficiency (fishing power) change over time, or if fish density or migration patterns are variable according to fisheries coverage which is usually the case (e.g. Godø 1994; Engås 1994; Pelletier 1998;; Marchal et al. 2001; Nielsen and Limborg 2009; Ulrich et al. 2012; ICES 2013d;e; Eigaard et al. 2014). Commercial fishing effort is normally concentrated on the highest densities of fish and not in the full stock distribution area of a stock resulting in unprecise (biased) abundance and density estimates. Commercial fishery only provides information on the exploitable component of the stocks in certain areas and seasons. In mixed fisheries targeting and coverage of the different species is very variable depending relative variation between species in overall and local fish densities, landing prices, fishing costs, fisheries regulations, etc. If assessment procedures pretend that catch rates from commercial catch and effort statistics are representative and adequate for estimating total stock abundance it can result in stock collapse because of continued high catch rates in stock concentration areas, i.e. the stock concentrate more and more, while the rest of the stock distribution area is depleted (Hilborn and Walters 1992; Beddington et al. 2007). To overcome the uncertainties inherent in commercial catch data, scientific bottom trawl surveys and trawl-acoustic surveys have become increasingly important for fish stock assessment and scientific management advice, and extensive research has been done on improving methods for reliable fish abundance and density estimates from surveys (e.g. Doubleday 1981; Doubleday and Rivard 1981; Godø 1990; Gunderson 1993; Godø 1994; Godø 1998; Pennington and Strømme 1998; Daug et al. 2002; Simmonds and MacLennan 2005; ICES 2013d;e). Survey effort involved is too small to peturb the fishery, the geographical and seasonal coverage is fully known, and the survey equipment can be held constant assuring standardized data and justifying assumptions on catchability does not change for technical reasons (although it may do so for biological or physical reasons) (Gulland 1988).

Similar to single stock assessments survey information is important for providing parameters to multi-species assessments on abundances and population dynamic parameters (e.g. ICES 2013e). Effective monitoring of marine communities and populations as well as marine habitat mapping is a prerequisite for ecosystem based management of marine areas where research survey information is widely used and play an important role (e.g. EC 1992; Fraser et al. 2007; Mehtälä and Vuorisalo 2007; HELCOM 2010; Cameron and Askew 2011; Katsanevakis et al. 2012). The ecosystem based approach to management is among other dependent on understanding fish foodweb trophodynamics and fisheries impacts on benhic communities, and here surveys may be the only data source available to estimate distribution and density of predators and prey species, as well as of important benthic species which are non-target species in the fisheries (e.g. Fraser et al. 2007). Survey data are furthermore important in monitoring and estimation of fish individual and population dynamic parameters as used in fisheries advice and marine population dynamic science including parameters of fish recruitment, growth, maturity, feeding, and mortality patterns, as well as migrations and changes in distribution and density patterns of the fish resources covering the full population (e.g. Lambert et al. 2009; Gascuel et al. 2014; Nielsen et al. 2012; Nielsen et al. 2013). Fisheries survey data are similar important for understanding the mechanisms of fish behaviour (e.g. Pitcher 1993; He 2010). Also, surveys provide important information to build into biological population dynamic modules in integrated multi-stock-multi-fisheries and bio-economic management evaluation models which are spatial and seasonal explicit (e.g. Bastardie et al. 2010; 2013; 2014). Here fish density and abundance data from surveys on spatial and seasonal explicit scale can be included in a

population dynamic module to evaluate resource availability dynamics and local stock harvesting and depletion by the different fisheries (metiers) using advanced bio-economic individual vessel based models evaluating management strategies for several exploited fish stocks and fisheries on spatio-temporal explicit basis (Bastardie et al. 2013; 2014). Such tools are for example used to evaluate impacts on stocks and fisheries of fishing closures, and establishment of by large, marine constructions such as bridges, tunnels and windmill farms.

The sea ecosystems evolves under many inter-connected and area specific pressures originating from natural and anthropogenic changes and there is an increasing magnitude and intensity of human pressures that cumulatively affect the seas (e.g. Halpern et al. 2008; Crain et al. 2008; Korpinen *et al.* 2012). Consequently, there is competition for space between marine sectors such as fishery, energy (windmill farms, oil extraction, wave energy platforms), shipping/transport, nature conservation, sand/gravel extraction, and recreational use (tourism, recreational fishery). This calls for integrated Marine Spatial Planning (MSP) and cross sector marine management (EC 2008b; HELCOM-VASAB 2010; EC 2013; Qui and Jones 2013). MSP and area based marine science and management is dependent on spatial and temporal high resolution information on fish (and larger invertebrate) distribution and density, which is available from research surveys most often covering the full population (or major part) in its full distribution area. This is to monitor impacts of the different sectors uses of the sea on the fish stocks, the ecosystem and the fishery. Reseach survey data are used in monitoring of ecosystem health, dynamics and development among other in relation to providing indicators and descriptors for Good Environmental Status (EC 2010) as well as anthropogenic pressure indicators for fisheries or other impacts on the ecosystem such as eutrophiccation and climate change or other marine sector pressures (e.g. Greenstreet et al. 1996; 1999; ICES 2011; EU STECF 2012; HELCOM 2013; Gascuel et al. 2014). As such fisheries research survey data are central in establishing knowledge basis for MSP and area based marine science and management (e.g. HELCOM-VASAB 2010; ICES 2011; EC 2013; Qui and Jones 2013).

Monitoring techniques of fish populations can be split into 2 broad categories: indirect and direct methods (Hilborn and Walters, 1992; Maunder and Punt 2004; Katsanevakis et al. 2012). Indirect methods are based on fishery-dependent data, such as catch and effort statistics and demographic (size and age) structure of the catch. Such methods are widely used (e.g. www.ices.dk; www.nafo.org; https://stecf.jrc.ec.europa.eu/) and allow the estimation of the biomass, abundance, and fisheries mortality of exploited marine fish stocks, either through dynamic pool methods (VPA, Virtual Population Analysis, and its modifications), statistical catch-at-age methods, or surplus production models. Direct methods are based on scientific research surveys and are aimed at avoiding the biases derived from the analysis of commercial catches. Typically, they are used to provide fishery-independent data on fish abundance and biomass in the sea and on the distribution by size and age of fish and shellfish. (Gulland 1988; Hilborn and Walters, 1992; Jennings et al. 2001). The direct methods can be split into removing, e.g. catch based (trawl, gillnet, longline, etc.), or non-removing, e.g. acoustic or visual (photographic, laser, etc.) methods (Katsanevakis et al. 2012). Typically, bottom otter trawls and beam trawls are used to monitor demersal fish populations, while acoustic methods and pelagic trawls are used to monitor pelagic fish populations.

If factors affecting survey detection efficiency are not identified and if possible separated it will be difficult to correctly interpret survey detection data, and changes in efficiency may be interpreted as changes in fish abundance and density. The present study will focus on efficiency of direct catch-based (mainly trawl) and acoustic-based survey methods.

Key issues influencing precision and accuracy of research survey esitmates (indices) as well as survey detection and catch efficiency

A main reason for conducting fisheries research is to study the dynamics of commercially exploited fish populations in relation to the dynamics of the fisheries and to provide the scientific basis and advice for managing fisheries in order to exploit our living resources sustainably (e.g. Hilborn and Walters 1992). The present thesis focus on aspects of providing representative, reliable and precise fisheries independent information on:

- fish abundance, density, distribution and migration according to age/size classes (as e.g. index of recruitment and population biomass of exploited fish populations);
- biological samples to study population growth (age, length), maturity (according to sex), and total and natural mortality;
- hydrographical data to study environmental conditions in fish habitats according to fish occurrence (e.g. temperature, salinity, oxygen, nutrients, etc.);

Given those aims it is necessary to consider key parameters and concepts related to and influencing the survey detection efficiency and the precision of CPUE estimates. This includes influence of survey design and effort stratification, survey data analysis methods in relation to data distributions and survey design, extrinsic factors affecting the survey detection and catch process and also the fish distribution and density patterns all impacting relative survey efficiency and precision, as well as methods for distinguishhing those factors. Furthermore, it is necessary to distinguish between the fish behavioural mechanisms and conditions, sensory modalities involved herein, as well as the extrinsic factors affecting fish behaviour, which all influence fish distribution and density patterns and accordingly survey efficiency and precision.

Table 2.1 Key issues influencing on precision and accuracy of research survey estimates. The chapters of the thesis where the different issues are covered are indicated as well.

1	Consideration of survey design and standardization of survey design and procedures	Ch. 1, 2-6
1a	Design and standardization of survey effort allocation	
1b	Design and standardization of survey equipment and its settings and operation	
1c	Design and standardization of sampling procedures from survey detection	
1d	Intercalibration of surveys with standardization of survey data time series	
2	Consideration of fish behaviour in relation to availability to the survey and behaviour in the survey detection and catch process	Ch. 1, 6
2a	Intrinsic factors influencing fish behaviour	
	Reactional behaviour according to the survey detection and catch process	
	Fear and avoidance behavior, aggregation behaviour according to herding	
2b	Extrinsic factors influencing fish behaviour	
	Natural behaviour (feeding, reproduction, agression, fear)	
	Physical, chemical, biological environmental factors influencing natural behavior	
	Physical, chemical, biological environmental factors influencing survey reactional behavior	
3	Survey design and stratification and sampling intensity	Ch. 1, 2-6
4	Evaluation of survey precision and sampling size	Ch. 1, 2-6
5	Survey data analysis methods	Ch. 1, 2-6
6	Consideration of survey data distributions	Ch. 1, 2-6

1.2 Objectives and scope

Overall aim

The aim of the thesis is to contribute to and improve the methods and knowledge basis for obtaining better and more accurate research survey estimates of fish density for use in marine fish population ecology and ecosystem based fisheries management.

This involves evaluation of trawl and hydro-acoustic research survey data with respect to analysis methods, stratification, standardization, and inter-calibration to estimate more precise, robust, and unbiased fish density and population parameters. The study focuses on factors affecting efficiency and precision of hydro-acoustic survey detection and demersal trawl survey trawl catch rates, i.e. fishing power and precision in relation to trawl catch per unit of effort (CPUE) and fish abundance from hydroacoustic backscattering.

Specific objectives and research questions:

The 1st purpose has been to estimate more precise fish distribution and density (patterns) using trawl and acoustic research survey methods, and by inter-calibration of trawl survey CPUE data (exemplified for juvenile Baltic cod in Chapter 2).

The 2nd purpose has been to improve and develop hydroacoustic research survey methods for more precise detection and discrimination of fish species according to fish size and orientation in the water (exemplified for gadoids with specific focus on juvenile Baltic cod in Chapter 3).

The 3rd purpose has been to estimate more precisely fish mortality, maturity, and growth parameters using trawl research survey density and distribution data (exemplified for Norway pout (*Trisopterus esmarkii*) in the North Sea in Chapter 4).

The 4th purpose has been to estimate more precisely pelagic fish migration according to density and distribution patterns using combined hydroacoustic, gillnet, and hydrographical research survey data (exemplified by Western Baltic herring in the Sound in Chapter 5).

The 5th purpose has been to synthesize and discuss analysis methods of research survey data and underlying data distributions, survey design and stratification, trawl survey inter-calibration, and estimation procedures and data processing methods according to survey precision and uncertainty (bias, sources of errors) for trawl and acoustic surveys as relevant for the above examples and the thesis research papers (discussed in Chapter 6).

Table 1. Key questions and parameters addressed by analysis of research survey information in the thesis and in specific chapters

Utility of survey information	**Population dynamic factor**	**Specific parameters**	**Specific papers with examples**	**Chapter / Objective**
Stock assessment; Multi-species interactions; Spatial planning;	Fish distribution and density, (and abundance);	Stock recruitment (R), trawl survey CPUE; acoustic back-scattering; trawl survey CPUE inter-calibration parameters; hydrographical parameters according to trawl CPUE and acoustic back-scattering density; prey, predator, and competitor density parameters;	Nielsen et. al. (2013). Localization of nursery areas based on comparative analyses of horizontal and vertical distribution patterns of juvenile Baltic cod; Nielsen et al. (2014). A spatial explicit statistical correlation model for estimation of fish density according to fish size within and between species from research survey data; Lewy, Nielsen and Hovgård (2004). Survey gear calibration independent of spatial fish distribution.	Ch. 2; Obj. 1;
		Acoustic target strength (TS), species specific acoustic back-scattering;	Nielsen and Lundgren (1999). Hydroacoustic *ex-situ* target strength measurements on juvenile cod (*Gadus morhua*); Lundgren and Nielsen (2008). A method for possible discrimination of juvenile gadoid fish by broad bandwidth backscattering spectra versus angle of incidence.	Ch. 3; Obj. 2;
Stock assessment; Spatial planning;	Natural mortality, maturity, and growth;	Fish natural mortality, growth, and maturity parameters;	Nielsen et al. (2012), Do Norway pout (*Trisopterus esmarkii*) die from spawning stress? Mortality of Norway pout in relation to growth, maturity and density in the North Sea, Skagerrak and Kattegat.	Ch. 4; Obj. 3;
Stock assessment; Spatial planning;	Pelagic fish density and distribution patterns to estimate broader scale migration;	Fish migration parameter; gillnet selectivity parameters; hydrographical parameters;	Nielsen et al. (2001a). Distribution, density and abundance of the western Baltic herring (*Clupea harengus*) in the Sound (ICES Subdivision 23) in relation to hydrographical features.	Ch. 5; Obj. 4;

1.3 Outline, concept and context of the issues addressed, methodology and improvement of knowledge basis

Estimation of juvenile fish distribution and density patterns using combined trawl and hydro-acoustic survey methods (exemplified for juvenile Baltic cod in Chapter 2)

So far there has been a gap in the available scientific knowledge regarding the distribution and abundance population dynamics of 0- and 1-group settled juvenile Baltic cod (*Gadus morhua*). An important reason for this gap is the lack of adequate coverage by research surveys and the fact that these life stages are not caught in commercial fisheries. The processes and pressures associated with these life stages and the variability in their distribution and abundance patterns as well as their nursery grounds are not well documented in terms of Baltic cod life cycle dynamics. The present thesis uses overlapping monitoring and combined research survey information and develops survey data analyses methods based on new survey design and effort stratification to be able to describe and more precisely estimate juvenile Baltic cod distribution and density patterns according to a row of influencing biological and physical factors including hydrographical factors, depth and density dependence (Chapter 2). The results can be used directly in stock assessment and fisheries management advice (recruitment estimates, abundance and density dynamics) and in broader marine management advice and spatial planning (e.g. environmental impact assessment (EIA) such as the Femern Belt fixed link in the Western Baltic Sea).
First of all, the approach has involved development of a new international and standardized stratified random ICES BITS trawl survey design covering more representatively the juvenile Baltic cod (Nielsen et al. 2001b; Nielsen et al. 2013). Also, it has involved development of an extended near field research survey design for BITS in the Femern Belt area of the Western Baltic Sea as a part of the baseline studies for impact assessment of the fixed link between Denmark and Germany in the Femern Belt (Nielsen et al. 2013). This enabled linking of survey time series and description of precision and variability in CPUE data between the broader standard BITS survey and a new local BITS survey with much higher coverage in time and space covering among other cod. Furthermore, it has involved establishment of standardized survey time series by development of a method for intercalibrating and linking new and former survey time series for different standard survey trawls (change of gear) covering among other juvenile cod (Lewy et al. 2004). On this basis, the overall approach has involved use of combined trawl survey information, acoustic survey information, and hydographical survey information (Nielsen et al. 2013), as well as involved development of different trawl survey data analysis methods with focus on cod (Nielsen et al., 2013; Nielsen et al. 2014). By use and comparison of results from the different types of surveys and by development of different trawl survey data analysis methods an improved, more precise, and more comprehensive analysis of the juvenile Baltic cod distribution and abundance patterns has been obtained and described through the thesis study. This integrated approach with combined and comparative analysis also considers individual research survey fishing power, efficiency, survey estimate precision, and selectivity according to size by species.
Methods for correlation analysis of Baltic cod and whiting (*Merlangius merlangus*) distribution patterns based on research surveys have been developed (Nielsen et al. 2014). This has been done to describe more precisely Baltic cod density and distribution patterns with a very high spatial and temporal resolution among other in a multi-species context involving fish prey, predator and competitor parameters. This has been supplemented with comparative feeding analyses of cod and whiting in the Western Baltic Sea (Ross et al. submitted). As a further supplement, comparative analyses of cod predator and herring and sprat (*Sprattus sprattus*) prey distribtion patterns in the

Baltic have been performed using acoustic research surveys (Nilsson et al. 2003). Hydrographical factors affecting Baltic cod recruitment such as salinity, temperature, oxygen and nutrient concentrations have as a supplement been analysed in Pecuchet et al. (*In press*). Fishing power analyses of Baltic cod for different commercial fishery fleets has furthermore been analysed in the publications by Marchal et al. (2001) and Nielsen (2000) and Bastardie et al. (2010), and an analysis of among other cod selective fishery in Kattegat is published in Kronbak et al. (2009). However, commercial fishery analyses are not in focus in the present thesis. (The references not underlined in Section 1.3 are supportive papers to the thesis where I am co-author).

Acoustic detection and discrimination of juvenile gadoids (exemplified for cod in Chapter 3)

Discrimination of gadoid species with overlapping distribution areas is not always straight forward in fisheries research sureys especially not for the gadoid juvenile stages (e.g. Nielsen et al. 2010; Lundgren and Nielsen 2008; Nielsen and Andersen 2001). As a prerequisite to carry out the analyses on juvenile cod distribution and density patterns, the approach has involved development and improvement of methods for direct hydroacoustic (survey) detection and discrimination of fish species according to size and orientation in the water (Chapter 3). The direct method for species and size discrimination of acoustic back-scattering provides better and more precise information on acoustic target strength (TS) measurements for use with hydroacoustic survey information. This has been used in advanced analyses of combined hydroacoustic and fishing gear (trawl, gillnet) survey information for direct and more precise estimation of fish occurrence, distribution, density, and abundance patterns with focus on gadoids, and more specific to evaluate vertical distribution of the juvenile Baltic cod and to distinguish and separate those from other acoustic targets such as sprat and herring in the Baltic (Nielsen and Lundgren 1999; Lundgren and Nielsen 2008). Several supportive papers on hydroacoustic fish distinction and 3D fish positioning with underwater video cameras have been published in Lundgren and Nielsen (2002), Lundgren et al. (2001), Nilsson et al. (2003) and Stage et al. (2008).

Estimation of fish mortality, maturity, and growth parameters using combined trawl research survey density and distribution data (exemplified for Norway pout in the North Sea in Chapter 4).

The mortality patterns of Norway pout (NP) (*Trisopterus esmarkii*) are not well understood. It has been suggested that NP undergo heavy spawning mortality. The very low–absent fishing activity in recent years has provided a unique opportunity to analyse the natural life-history traits of cohorts in the NP stock in the North Sea. The present thesis uses combined research survey information on catch rates and sampled biological data (Age-Length-Sex-Maturity-Keys) to calculate more precise abundance indices from the ICES IBTS trawl surveys to analyse cohort total and natural mortality correlated with sexual maturity, sex, growth, and intraspecific stock density (Nielsen et al. 2012; Lambert et al. 2009; Sparholt et al. 2002a;b) (Chapter 4). The North Sea–Skagerrak–Kattegat Norway pout stock is an important food source for commercially important fish species, such as cod, saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), and whiting. Therefore, this small, short-lived species is an important prey organism in the North Sea ecosystem (Sparholt et al. 2002a). In addition, the NP stock is usually a direct target of a significant small-meshed fishery for reduction (industrial) purposes. Accordingly, it is important in context of fisheries management and scientific management advice to know and obtain more precise parameter estimates of the natural mortality, maturity, and growth patterns for this stock when applying an ecosystem based approach to fisheries management. The new mortality, maturity and growth parameters have been implemented into the stock assessment, management advice (e.g.

ICES 2013e) and fisheries management strategy evaluation for the NP stock in the North Sea (Vinther and Nielsen 2013; Nielsen and Vinther (*In Submission*)). Also, mortality is relevant in relation to gear selection for Norway pout (Eigaard et al. 2012). The thesis discusses precision of abundance indices, fishing power and selectivity in the trawl research surveys according to different NP age groups and life stages. The significantly increasing cohort mortality with age associated with spawning maturity and specific growth patterns related hereto cannot be explained by selectiveness in the fishery, potential size-specific migrations out of the area, higher predation pressure on older individuals, or differences in survey fishing power by NP age from before to after spawning and that it is higher in the main spawning areas than outside (Nielsen et al. 2012).

Estimation of pelagic fish density and distribution in a narrow survey area in relation to broader scale migration patterns using combined hydroacoustic, gillnet, and hydrographical research survey information (exemplified by Western Baltic herring in the Sound in Chapter 5).

The migration patterns of the Western Baltic spring spawning herring *(Clupea harengus)* (Rügen Herring Stock, RHS) is not fully documented and quantified. Results from tagging experiments and fishery information indicate that the Sound (ICES SD23) is a major over-wintering area for this stock, and that the main component of herring in the Sound is from this stock. These studies showed a typical migration pattern of RHS between the main spawning grounds around Griefswalder Bodden to the feeding areas, one north-westward migration extending to the Kattegat / Skagerrak / North Sea area and one eastern migration extending to east of Bornholm and the western part of Hanö Bay in the Baltic Sea. The present thesis developed specialized surveys and makes use of integrated acoustic survey information (Nielsen et al. 2001a; Nielsen et al. 1999), gillnet survey information (Poulsen et al. 2000) and hydrographical survey information to analyse herring abundances in the Sound and to obtain more precise estimates of distribution, density and migration patterns of the stock according to hydrographical parameters (Nielsen et al. 2001a; Nielsen et al. 2001c) (Chapter 5).
The western Baltic spring spawning herring stock is a significant resource for the Danish, German, Norwegian and Swedish commercial fishery in the Baltic Sea, Kattegat-Skagerak, and to a lesser extent in the North Sea, and accordingly the results of the present investigations are directly used in stock assessment and fisheries management advice for this stock. Furthermore, it has been used in broader marine management advice and spatial planning context covering among other environmental impact assessment (EIA) the Sound Bridge and Tunnel between Denmark and Sweden in the Western Baltic Sea. During a 5 year period from 1993-1998, 27 hydroacoustic echo integration surveys with a standard set of acoustic transects were carried out in the central Sound from Helsingor-Helsingborg (north) to Drogden (south) covering all seasons of year.
The approach has first of all involved development of a stratified integrated hydro-acoustic, experimental gillnet, and hydrographical survey (Nielsen et al. 1999) covering representatively and intensively the different size groups and life stages of herring in the Sound area. From concurrent biological sampling with scientific multipanel gillnets equipped with a wide range of mesh sizes and/or with large, pelagic trawls, species composition and size and age were estimated (Nielsen et al. 2001a) as well as gillnet selectivity for herring (Poulsen et al. 2000). The results were compared with concurrently sampled hydrographical (CTD) data and data on water currents. The aim of the investigations has been to estimate more precisely biomass levels of the herring in the Sound over several years in all seasons of year to estimate more precisely the duration of over-wintering in the Sound in relation to the overall stock migration patterns. Furthermore, specific distribution and density patterns of herring compared to hydrographical features and depth in different areas, seasons of the year and between years in the Sound have been investigated. This includes whether

water inflows to the Baltic may trigger southwards migration of the spring spawning herring from the Sound to the spawning grounds. (Nielsen et al. 2001a; Nielsen et al. 2001c). These investigations of the RHS migrations have been followed up through the Femern Belt Science Provision Project (2009-2012) analyzing potential impacts of a fixed link in the Fehmarn Belt between Denmark and Germany (Clausen et al. (*In Submission*)). As a relevant supplement vertical migration and dispersion patterns of Baltic sprat and herring schools at dusk have been investigated in Nilsson et al. 2003). Furthermore, the influence of hydrographical factors (temperature, salinity, oxygen, nutrients) on among other RHS recruitment has been investigated in Pecuchet et al. (*In press*). The thesis evaluates and discusses fishing power and selectivity in the different types of research surveys for herring.

Discussion (Chapter 6)

To cover the objectives, different issues concerning the development, design, combined use, and detection efficiency of research survey information, and different methods to improve research survey information to provide more precise and accurate survey estimates of population parameters, have been investigated as described in Chapters 2-5. The thesis contributes to the overall knowledge and development of research survey methodology, survey analysis methodology including evaluation of survey detection and catch efficiency and precision and factors affecting it, as well as the advanced use and analysis of combined and multi-purpose survey information. It is necessary on case specific basis to consider influencing factors on precision of survey detection and catch efficiency covering different types of surveys such as trawl surveys, integrated acoustic and trawl surveys, and gillnet surveys associated with hydrographical surveying.

The discussion synthesize and discuss analysis methods of research survey data and underlying data distributions, survey design and stratification, trawl survey inter-calibration, and estimation procedures and data processing methods according to survey precision and uncertainty (bias, sources of errors) for trawl and acoustic surveys as relevant for the above examples and the thesis research papers (Chapter 6). It integrates the methodological principles of research surveys with respect to estimating research survey catch rates or acoustic backscattering and the precision of survey estimates. Here survey data analysis methods and assumptions on survey data distributions in relation to the precision and accuracy of survey estimates, as well as in relation to estimation of detection efficiency, is addressed. There is distinguished between assuming independence between survey observations or integrating correlation between survey observations across species, size, area and season. Furthermore, the discussion is integrating survey design and standardization of survey design and procedures. This covers standardization of design with respect to effort (haul or detection) allocation and stratification, as well as inter-calibration of surveys with standardization of survey data time series.

The survey data analysis methods and survey sampling stratification used in the thesis papers are integrated in this discussion including the supportive literature published in relation to the main thesis papers. As such, the present studies are set into perspective of state of the art, and presented in context of survey detection efficiency, factors involved herein, and the extent to which they are taken into consideration when samling and analysing survey data in relation to precision.

Chapter 2

Development, use and analysis of combined research survey information to describe juvenile Baltic cod distribution and density patterns

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Localisation of Nursery Areas Based on Comparative Analyses of the Horizontal and Vertical Distribution Patterns of Juvenile Baltic Cod (*Gadus morhua*)

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Abstract

Knowledge of the spatial distribution of juvenile cod is essential for obtaining precise recruitment data to conduct sustainable management of the eastern and western Baltic cod stocks. In this study, the horizontal and vertical distribution and density patterns of settled juvenile 0- and 1-group Baltic cod are determined, and their nursery areas are localised according to the environmental factors affecting them. Comparative statistical analyses of biological, hydrographic and hydroacoustic data are carried out based on standard ICES demersal trawl surveys and special integrated trawl and acoustic research surveys. Horizontal distribution maps for the 2001–2010 cohorts of juvenile cod are further generated by applying a statistical log-Gaussian Cox process model to the standard trawl survey data. The analyses indicate size-dependent horizontal and distinct vertical and diurnal distribution patterns related to the seabed topography, water layer depth, and the presence of hydrographic frontal zones (pycnoclines) as well as intraspecific patterns in relation to the presence of adult cod. The extent of the nursery areas also depends on the cod year class strength. Juvenile cod ($\geq$3 cm) are present in all areas of the central Baltic Sea (CBS), showing broad dispersal. However, their highest density in the Baltic Basins is found at localities with a 40–70 m bottom depth in waters with oxygen concentrations above 2 ml $O_2.l^{-1}$ and temperatures above 5°C. The smallest juveniles are also found in deep sea localities down to a 100 m depth and at oxygen concentrations between 2–4 ml $O_2.l^{-1}$. The vertical, diurnally stratified and repeated trawling and hydroacoustic target strength-depth distributions obtained from the special surveys show juvenile cod concentrations in frontal zone water layers (pycnocline). However, the analyses indicate that in the CBS, juvenile cod of all sizes do not appear to aggregate in dense schooling patterns, which differs from what has been reported from the North Sea.

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Introduction

The changes in hydrographic features and potential changes in cod spawning areas and nursery ground locations over time, together with the resulting recruitment variability and possibly different recruitment regimes [1,2,3,4,5], heavy exploitation by fisheries and likely changes in migration at age between the two Baltic cod stocks [1,6,7] complicate the long-term management of the stocks [8,9,10]. This situation should be seen in the light of the fact that the adult cod in the eastern Baltic Sea are distributed at one of their environmental limits regarding salinity and oxygen tolerance [11,12] and that their abundance has changed considerably in historical times as a result of variations in the environment [1,3,13,4,5,14]. Extensive long-term fluctuations in stock recruitment have proven to depend on climate-driven hydrographic conditions and regime shifts [15,1,2,3,16,4,6,17,7]. All of these factors call for deeper investigations of juvenile cod distribution patterns and variations in the central Baltic Sea.

In general, there is a gap in the available scientific knowledge regarding the biology and population dynamics of 0- and 1-group settled juvenile Baltic cod (*Gadus morhua*) [18,19,3,14,7,17]. An important reason for this gap is the lack of adequate coverage in research surveys and the fact that these life stages are not caught in commercial fisheries [20,7,21]. The processes and pressures associated with these life stages and the variability in their distribution and abundance patterns as well as their nursery grounds are not well documented in terms of Baltic cod life cycle dynamics [22,3,1,7].

In 2001, the EU research project ISDBITS (see references) introduced a completely revised international standardized BITS survey (ICES Baltic International Trawl Survey) [23,20,21] with the aim to introduce new demersal survey gear and a new stratified random sampling survey design, expanding seasonal and geographical sampling to obtain better coverage of cod distribution areas in all life stages. In particular, a focus is concentrated on more efficiently covering of the settled stages of juvenile cod by increasing the survey fishing power for these life stages [23,20]. Accordingly, the quality of the survey indices has increased, and more recruitment and abundance at age data at a higher coverage have been obtained for use in ICES Baltic cod stock assessments

for management purposes and in research on population dynamic [7,21].

In the traditional BITS, the participating nations used very different trawls, usually equipped with large bobbins, causing smaller cod to escape under the footrope [24]. ISDBITS employs new internationally standardized survey trawls of the commercial TV3 type mounted with rubber disc bottom gear exhibiting close seabed contact and being robust to the CBS bottom topography [23,20,21]. Furthermore, statistically robust and standardized inter-calibration methods to link old and new survey data time series have been developed and implemented to estimate the trawl survey efficiency and fishing power (and selectivity) as well as to link indices obtained using different sizes of the new standard gear [20,21]. After 12 years of implementation of this new survey design, the understanding of juvenile cod distribution patterns and of the spatio-temporal patterns in recruitment dynamics can now be improved via thorough analyses of the obtained BITS data.

Such analyses should contribute to validating the predictions of the advanced 3D- hydrodynamic drift model currently applied in the Baltic Sea [22,3], where the transport patterns for eastern Baltic cod eggs and larvae according to the spawning area and time have been simulated for the periods 1986–99 and 1979–2004. The model predicts which habitats show a high probability of successful settling of early demersal stage juvenile cod, depending on the oxygen saturation. The predicted habitats are located in the shallow-water areas at the edges of the basins (40–60 m bottom depth) down to where the halocline hits the bottom, while the settlement probability in the deeper central parts of the basins is low due to the minimum oxygen requirements for successful settling. These predictions are to be verified based on the present updated observed distributions from pelagic and demersal trawl surveys because previous BITS, Baltic hydroacoustic research surveys and commercial fishery data [7,21] have not covered juveniles adequately.

Among the explanatory factors, interspecific relationships and potential intraspecific density dependence may play a role in the distribution patterns of Baltic cod in relation to other Baltic fish species, but neither factor is well understood [25,17]. There is temporal variation in biological interactions due to predation by cod and food availability related to prey stocks such as sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the Baltic, and size dependent predation can be central in relation to cod recruitment because cannibalism has been documented as an impacting factor in certain periods [26,27,28,18,14,29,17]. The levels of cannibalism are dependent on the abundance of juveniles and larger cod predators, their overlap in distribution, and the availability of alternative prey items for larger cod, such as sprat and herring [30,18,29]. Additionally, in the western Baltic Sea, there are competing gadoid predators in the form of whiting (*Merlangius merlangus*) [7]. Consequently, the present investigation of juvenile cod distribution dynamics in relation to cod predators is relevant.

Kristensen [31] and Lewy and Kristensen [32] estimated North Sea cod distribution patterns with their Log-Gaussian Cox Process (LGCP) model, determining correlations in densities using a statistical approach based on spatial correlations between observations from surveys and fisheries according to age. A length-based stochastic model of single-species stock dynamics including densities [33] has been applied for Baltic cod based exclusively on survey data; however, this model is not spatially explicit. An extension of the LGCP model was applied to mackerel (*Scombrus scombrus*) larvae survey data [34] based on additional temporal covariance in spatial distributions. The LGCP model provides densities with high resolution in time and space for survey data. In the present study, a similar extension of the LGCP model is applied to the BITS data, but with a further extension in the form of following individual cohorts to describe the distribution and density patterns of settled 0- and 1-group Baltic cod.

The below 0-hypotheses (where the hypotheses are not mutually independent) regarding the settled Baltic juvenile cod distribution, density and abundance patterns are tested in the present study based on the new, revised BITS data, with a new survey design and recent improved survey data analysis methods. The analyses mainly cover the life stages before recruitment to the fishery, and in the ICES stock assessments.

H01: Settled juvenile Baltic cod are only present in shallower (more oxygen saturated) areas down to a 60 m depth in the Baltic Sea, e.g., at the edges of the Baltic basins; i.e., juvenile Baltic cod exhibit distinct and limited geographical nursery areas, without considerable variation over years.

H02: Settled juvenile Baltic cod aggregate in dense schools and show schooling behaviour, as observed for juvenile cod in the North Sea.

H03: Settled stages of juvenile Baltic cod do not show distinct vertical distribution patterns related to hydrographic vertical zoning.

H04: There is no dependency of the occurrence of settled juvenile cod in relation to larger cod (potential predator size group) or of their distribution in relation to year class strength.

Materials and Methods

Survey coverage and stratification

The BITS survey manual [21] describes the revised (2001 and thereafter) standardized and stratified random BITS TV3-bottom-trawl surveying and sampling methods, including the format of the BITS data which are available at the ICES DATRAS database (www.ices.dk). The BITS survey is stratified according to ICES subdivision (SD) and depth. The geographical coverage of the BITS cod trawl sampling data analysed in this study corresponds to ICES SDs 24–29, which represent the different Baltic basins and deeps which are important ecosystem units in cod spawning and recruitment ecology, i.e. the Arkona Basin (SD24), the Bornholm Basin area and around Bornholm, and the Bank areas SW of Bornholm, as well as the Hanö Bay (SD25), the Gotland Basin area (SD28), and the Gdansk Deep area (SD26) (see example in Fig. 1). Additional trawl sampling was performed during specialised integrated multi-task trawl and acoustic juvenile cod distribution surveys repeated in 1995, 1997 and 1998 (Table 1; [35]) as a part of the EU-FP4-AIR2-94-1226 Baltic Cod Recruitment Project. The repeated surveys were a part of more than 14 surveys (1994–1998) under the project with broad sampling of biological and physical-chemical oceanographic and acoustic data (Fig. 2) covering different seasons and areas of the CBS. These surveys targeted the early life stages of cod, including the eggs, larvae, and 0- and 1-group metamorphosed juveniles. For the repeated surveys (1995, 1997, 1998) selected areas of the Baltic Proper (SDs25–26) were subdivided into three main types of cod habitats according to physical and biological environmental conditions and bottom depths: Area 1: A shallow-water area southwest of Bornholm and the Bornholm Basin at the Rønne Bank, Adler Ground, and Oder Bank (SW Baltic Sea); Area 2: A medium-depth area in the Gdansk Deep area located southeast of the Bornholm Basin (SE Baltic Sea); and Area 3: A deep-sea area

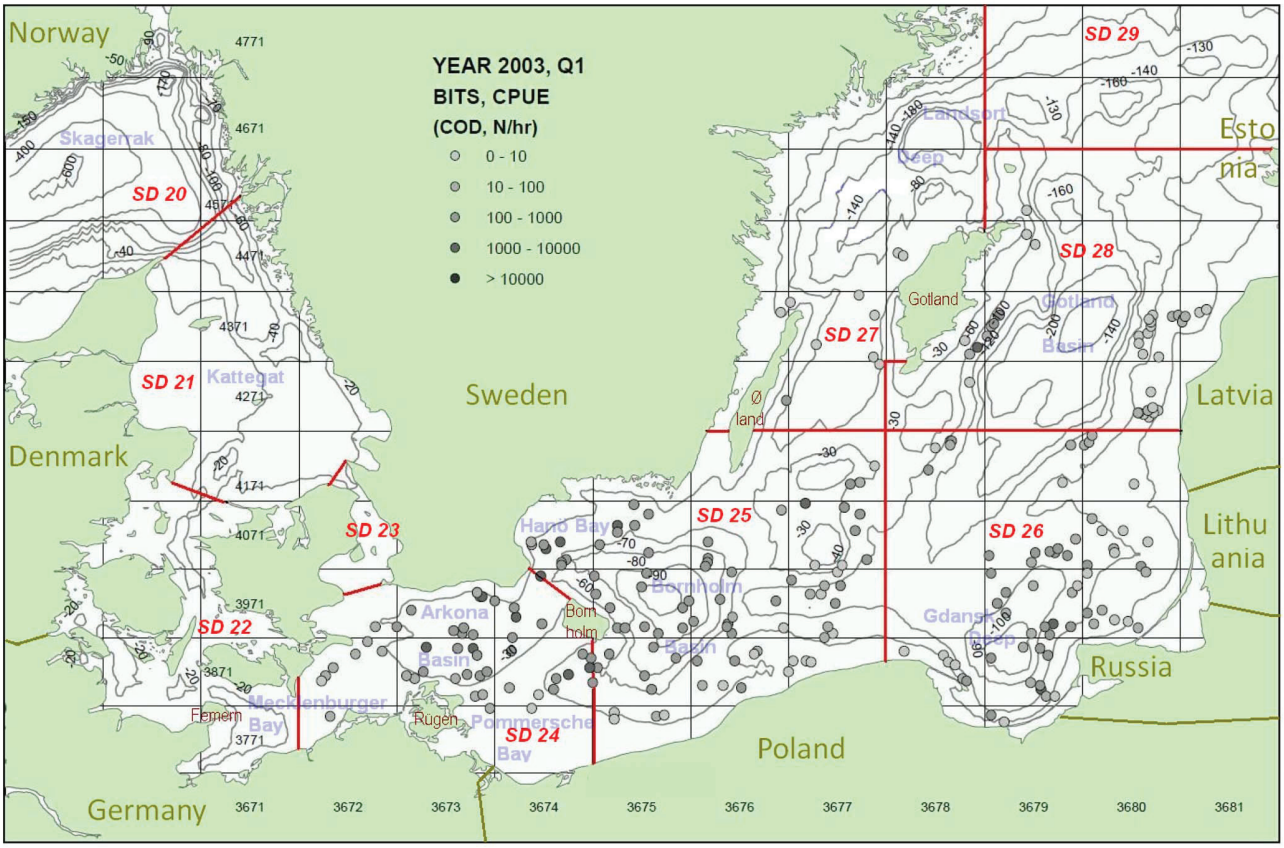

Figure 1. Investigation area for juvenile cod distribution and coverage of the stratified random and standardized ICES BITS trawl survey with new survey design according to Nielsen *et al.* (2001) and Lewy *et al.* (2004) including station specific catch rates of cod (example from the 1st quarter 2003 survey).
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in the Bornholm Basin area east of Bornholm and north of the other areas. (Fig. 2; Table 1). Here, he monitoring covered trawl sampling, the sea bed topography, and hydrographic features including variation in vertical physical frontal zones (the presence and depth of the pycnocline) based on CTD (Conductivity Temperature Depth Profiler) measurements. The specialized survey data are stored in the DTU Aqua databases and can be made available through DTU Aqua IT Management (www.aqua.dtu.dk). The benthic biological habitats were also characterised according to the density patterns of major food items for juvenile cod, e.g., the abundance of mysids (*Mysidae*), measured via hydroacoustic methods.

Biological trawl sampling

The fish sampling was designed according to standard procedures presented in the BITS Manual [21]. During the 1998 specialised survey in particular, standardized and depth-stratified fishery sampling was performed through repeated day and night hauls at the selected localities (Table 1; Fig. 2) covering 2 full days and 2 nights per locality per survey. This sampling was performed with a large, combined demersal and pelagic EXPO trawl equipped with small bobbins and using a pelagic young fish trawl (IYGPT), both with a stretched codend mesh size of 16 mm, in addition to a smaller-meshed pelagic MIK ring trawl to a lesser extent. Nearly all hauls performed with the EXPO and IYGPT trawls were double oblique (V-shaped) hauls covering a specific targeted vertical water layer (Table 1) as well as the sea bottom, when performing targeted bottom hauls. As such, isolated demersal and pelagic hauls in specific water layers were conducted to identify juvenile cod vertical distribution patterns. The active fishing time with the EXPO trawl was usually 40 minutes, of which 25 minutes was devoted to trawling in the targeted vertical water layer. The hauling speed was between 3.4 and 4.1 knots, typically ranging from 3.8–3.9 knots. The trawl gap varied from 6 m, at the bottom, to 8 m, when pelagic, and the trawl width was between 90 and 105 m (typically 100 m). The details of the BITS and specialised surveying procedures are shown in Figures 1–2 and Table 1. In general, cod were not caught in the pelagic IYGPT and MIK trawls during the specialised surveys, so only the EXPO activities are shown in Table 1.

Hydrographic CTD recording

To localise the pycnocline and determine the near-bottom salinity, temperature, and oxygen concentration at the trawling localities a vertical CTD profile of the water column structure was obtained for each trawling event using a SEABIRD SBE 911+ model CTD with standard probes for pressure, conductivity, temperature, and oxygen (Table S1 in File S1). The profiles covered the entire vertical water column, including the near-bottom layer. The CTD probes were calibrated before each survey, and cross-checking was performed by taking salinity and oxygen water samples using a GO rosette sampler during up-casts. Salinity of the water samples was measured with a Guildline Portasal 8410A. The oxygen profiles were corrected by linear

Table 1. Division of fishing stations at the repeated specialized surveys with small meshed EXPO trawl by locality, time of day and hauling layer during at the R/V Dana winter surveys December 1998 (DS1698), January 1997 (DS0197), and December 1995 (DS1295).

Stratum	Time	Layer DS1698	Stations DS1698	Layer DS0197	Stations DS0197	Layer DS1295	Stations DS1295
Shallow water locality	Night	Bottom	10, 32	Full layer	7		
54.43N 14.32E		Surface	(7), (8), 29, 36, 38				
	Day	Bottom	21, 24, 45			Full layer	81
		Surface	18, 42				
Medium deep locality	Night	Bottom	59, 82	Full layer	11, 13	Full layer	107, 109, 110, 111
54.35N 15.22E		Medium layer	(58), 62, 80, 89				
		Surface	57, 61, 78				
	Day	Bottom	70, 73, 99, 103	Full layer	78, 80, 81, 82, 84		
		Medium layer	68, 97				
		Surface	66, 95				
Deep sea locality	Night	Bottom	128, 169				
54.56N 15.40E		Medium layer	126, 170				
		Surface	124				
	Day	Bottom	117, 158				
		Medium layer	115, 160				
		Surface	113, 119, 161				

doi:10.1371/journal.pone.0070668.t001

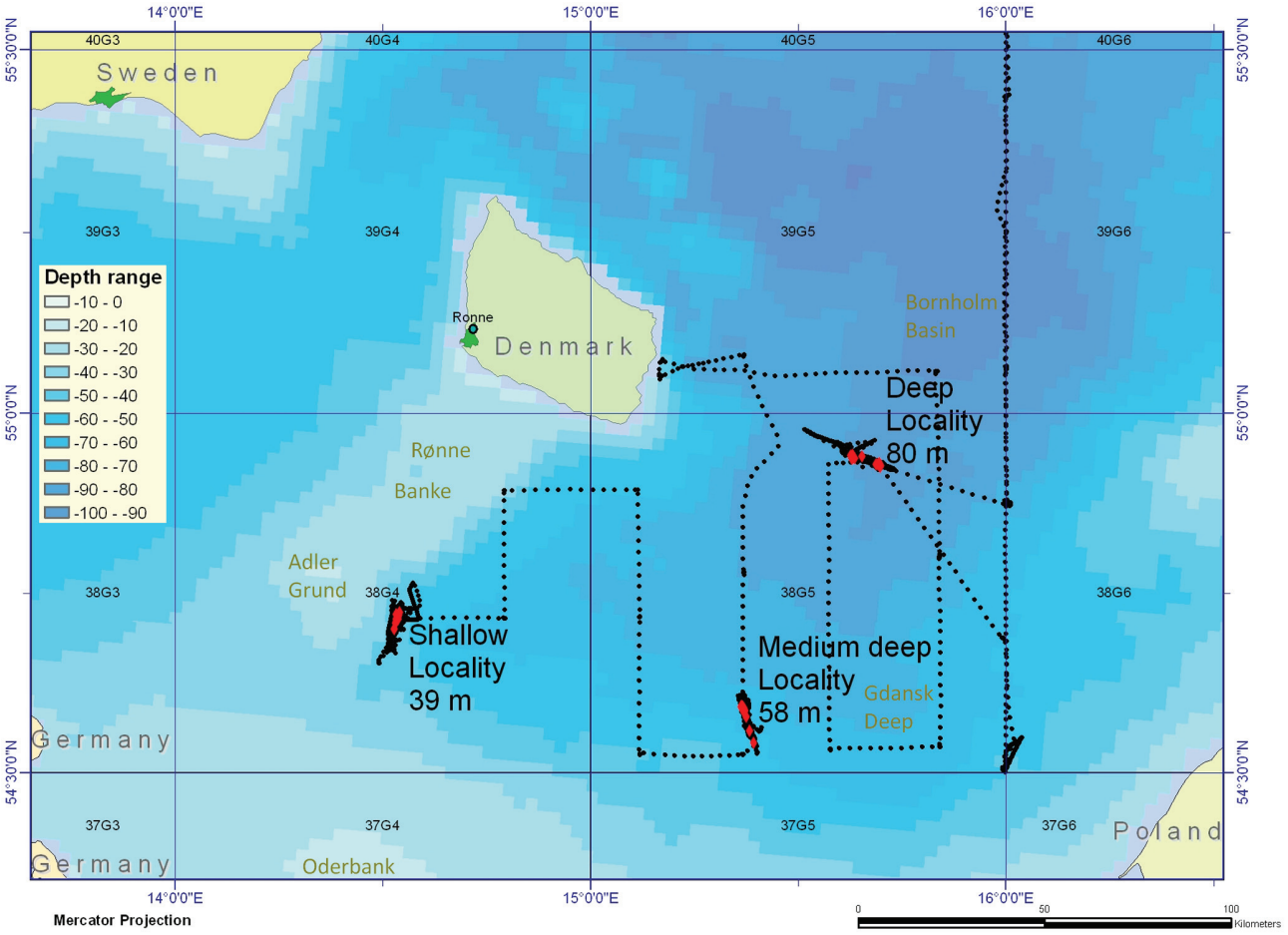

Figure 2. Coverage and topography of the selected stations of the 3 types of central Baltic localities (shallow Bank, medium deep, and deep basin locality) investigated by intensive and combined trawl, hydrographic and hydroacoustic transects between localities (including 2 days and 2 nights continuous sampling at each locality) during the specialized surveying in 1998.
doi:10.1371/journal.pone.0070668.g002

regression based on results from Winkler titration of the oxygen water samples.

Hydroacoustic data recording

Acoustic data were collected using the Simrad EY500 portable scientific 38 kHz split beam echosounder system (version 5.0 [36]) with an ES38-B-type hull-mounted transducer placed at 6 m depth below the sea surface. The parameter settings are shown in the Table S1 in File S1. An external power supply was employed to increase the pulse power to 987 W to improve the signal-noise ratio. The parameters for sound speed and absorption coefficient were set to 1450 m s^{-1} and 4 dB km^{-1}, respectively, to account for the average values below the transducer derived from the salinity and temperature measurements. The system was calibrated before each survey according to the standard copper sphere technique [37,38,39,40,41]. Transects of raw split-beam data were collected along the entire hauling transect at all trawl stations during the specialised surveys to obtain spatially overlapping and activity-specific acoustic profiles that were directly comparable to the trawl sampling data (Fig. 2). Supplementary acoustic data collection (Fig. 2) was performed between the trawl stations. The raw data were analysed with the Echoview Version 4.6 software. The original target strength (TS) values produced by the echosounder were not used. Instead, the targets were redetected and the TS values recalculated using the Single-targets Method 1 operator in Echoview (http://www.echoview.com/support/echoview-technical-manual). This operator applies an improved version of the algorithm implemented in the Simrad EK500 software to detect single targets from echo data [42,43,44,45]. The analyses were performed for the water layer from 3 m below the transducer to 0.5 m above the bottom echo.

Comparative data analysis of juvenile cod distribution patterns

First, a size-based generalised linear model (GLM) analysis was applied assuming negative binomial distributions and over-dispersion [46]. Then, the statistical LGCP correlation model was applied on the same data to determine the high-resolution density patterns of the 0- and 1-group cod cohorts through spatial and temporal correlations between survey observations based on previously described methodology [34,31,32]. In the present application, the LGCP model was further advanced to also follow the correlations within individual cod cohorts. The output from these statistical analyses of the density and distribution patterns was compared with the ICES assessment working group [7] cod year class strength estimates. Finally, the data analysis comprises an integrated analysis of the combined trawl catch data (Table 2)

Table 2. Year class strength of eastern Baltic cod by year.

Year/Year Class	Inflow Strength into the Baltic	Recruitment age 2, XSA, ICES WGBFAS	Recruitment age 2, SAM, ICES WGBFAS	0-group BITS Q4 index from ICES DATRAS	1-group BITS Q1 index from ICES DATRAS	2-group BITS Q1 index from ICES DATRAS	Year Class Strength
2000	Weak	122472	116891	13783	42662	271924	(Weak)
2001	Weak	112745	95130	7516	38347	61747	Weak
2002	Weak	115077	99808	2470	10267	74005	Weak
2003	Strong	164235	138552	57669	83266	238898	Strong
2004	Weak	131041	129444	10838	58983	110839	Weak
2005	Weak	143846	140646	9509	6559	160561	Weak
2006	Weak	158464	152665	22907	58475	297516	Strong
2007	Weak	161770	156217	9867	36435	213619	(Strong)
2008	Weak	192503	177549	14774	28146	173658	(Strong)
2009	Weak	205390	192914	8107	7444	160703	(Strong)
2010	Weak		184795	3090	10105	171725	(Strong)
2011	Strong			11694	6788		?

Recruitment at age 2 in thousands from ICES WGBFAS, and CPUE index at age 0 and 1 by quarter from the ICES BITS DATRAS Database from spring 2012. Sources: ICES WGBFAS [5]; ICES DATRAS Database July 2012 (www.ices.dk). In the period 2000–2005 there were strong inflow events in spring 2003 and Nov/Dec 2011 of saline and oxygenated North Sea water into the Baltic while the inflow was weak in the rest of the period. Sources: [23,49,50,24,51], http://www.smhi.se/en/News-archive/improved-oxygen-conditions-in-the-baltic-deep-water-1.21801#bottom.

doi:10.1371/journal.pone.0070668.t002

and hydroacoustic data from the specialised surveys, with a focus on the 1998 sampling targeting the vertical distribution of juvenile cod.

Generalised linear model statistical data analysis

Prior to analysis, the raw BITS catch data for each haul were grouped into length groups and classified according to the year, quarter of the year, area (locality), and seabed depth (Eq. 1):

$$\mathrm{N(len)_h} = \sum_{l=l_{min}}^{l_{max}} N_l \qquad (1)$$

where N_l is the number of cod caught per haul per 1 cm length group, l, and $\mathrm{N(len)_h}$ is the number of cod caught per haul (h; by survey) per length group. The group class length is $\mathrm{len} = int((l_{min} + l_{max})/2)$, where l_{min} is the smallest length group, and $l_{max} = l_{min} + \Delta l$ is the largest and where Δl-values of 5 or 10 cm were used. The raw catch data per haul were used as a proxy for the catch per unit of effort (CPUE) because the standard haul duration was 30 min, and hauls with a duration of less than 25 min or more than 35 min were excluded from the analyses (only few hauls). The data were not standardized to 1-hour hauls because the negative binomial distribution (see below) was not well suited to handle such standardisation. In the GLM analyses, the dependent variable CPUE was categorised into 5 cm cod length groups (Eq. 1; Table 3; Table S2 in File S1). In some instances, the consistency in length dependency was tested with an alternative 10 cm length stratification of the juvenile cod. The investigated area was surveyed using standard TV3 trawls of two different sizes in different ICES subdivisions (a small TV3 in SDs24–25 and a large TV3 in SDs25–29). Gear calibration was performed [23,20], and conversion factors between the two trawls according to species and fish length groups were previously reported [20]. For cod, CPUE values obtained with the small TV3 trawl were converted to equivalent CPUE values for the large TV3 trawl with the following conversion factors: length less than 10 cm, 1/1.68; 10–15 cm (10 cm incl. and 15 cm excl.), 1/1.06; 15–20 cm, 1/1.15; 20–25 cm, 1/0.98; 25–30 cm, 1/0.91; 30–35 cm, 1/0.80; 35–40 cm, 1/0.81; 40–45 cm, 1/0.61; 45–50 cm, 1/1.12; 50 cm and larger, 1/1.29.

The analysis covers all of the cod caught in more than 4,750 hauls for the full revised-design BITS survey time series (2001–12), with a total of 1,560 individuals in the 0–5 cm length group, 25,536 in the 5–10 cm group, 41,042 in the 10–15 cm group, 115,153 in the 15–20 cm group, and more than 1.3 million above 25 cm. The GLM applied to estimate parameters (Eq. 2) and test hypotheses for each length group employed a negative binomial distribution and log (the canonical link function) of the CPUE as a linear function of the parameters tested, i.e., assuming that the logarithm of the mean is linear (GENMOD procedure in the SAS vers. 9.2 statistical software [47,48]). This allows for inclusion of 0-observations (CPUE rounded up to the nearest integer), i.e., zero catches of cod by length. If the assumption of negative binomially distributed data does not hold, an over-dispersion parameter is estimated. The full model, which defines how the expected catch value (E(CPUE); referred to as the cod density here) by length group depends on the descriptive factors and class variables, is given in Equation 2.

$$\log(E(CPUE))_L = \alpha + \beta_{year} + \gamma_{quarter} + \delta_{area} + \theta_{depth} + \mu_{density} \qquad (2)$$

Table 3. Generalized linear model maximum likelihood parameter estimates of CPUE by using the SAS GENMOD Procedure for the statistical model 1 (Eq. 2), and the negative binomial dispersion parameter estimated by maximum likelihood.

				Wald 95%		Wald				Wald 95%		Wald				Wald 95%		Wald				Wald 95%		Wald	
Statistic		Estimate	SE	Confidence Limits		Chi-Sq	Pr> ChiSq	Estimate	SE	Confidence Limits		Chi-Sq	Pr>ChiSq	Estimate	SE	Confidence Limits		Chi-Sq	Pr> ChiSq	Estimate	SE	Confidence Limits		Chi-Sq	Pr>ChiSq
Length Group		3 cm	3 cm	3 cm	3 cm	3 cm	3 cm	8 cm	8 cm	8 cm	8 cm	8 cm	8 cm	13 cm	13 cm	13 cm	13 cm	13 cm	13 cm	18 cm	18 cm	18 cm	18 cm	18 cm	18 cm
Parameter																									
Intercept		−1.6816	0.5891	−2.8363	−0.5270	8.15	0.0043	0.4981	0.2635	−0.0183	1.0146	3.57	0.0587	−0.4266	0.2503	−0.9173	0.0640	2.90	0.0883	2.0371	0.2162	1.6134	2.4608	88.79	<,0001
Year	2001	0.7497	0.4895	−0.2098	1.7092	2.35	0.1257	0.8443	0.2202	0.4127	1.2758	14.70	0.0001	1.4525	0.2086	1.0436	1.8614	48.46	<,0001	0.1684	0.1901	−0.2042	0.5410	0.78	0.3757
Year	2002	−0.0285	0.5226	−1.0528	0.9957	0.00	0.9565	0.6211	0.2245	0.1810	1.0612	7.65	0.0057	0.3762	0.2166	−0.0483	0.8007	3.02	0.0824	0.4831	0.1870	0.1165	0.8496	6.67	0.0098
Year	2003	0.8708	0.4955	−0.1004	1.8420	3.09	0.0789	1.3507	0.2290	0.9019	1.7996	34.79	<,0001	1.2338	0.2222	0.7984	1.6692	30.84	<,0001	0.6233	0.2040	0.2234	1.0232	9.33	0.0022
Year	2004	1.1931	0.4876	0.2374	2.1487	5.99	0.0144	1.0436	0.2220	0.6085	1.4786	22.10	<,0001	1.8225	0.2123	1.4065	2.2386	73.72	<,0001	1.2371	0.1874	0.8699	1.6044	43.59	<,0001
Year	2005	0.1071	0.4957	−0.8645	1.0787	0.05	0.8289	−0.4994	0.2220	−0.9345	−0.0643	5.06	0.0245	0.0149	0.2126	−0.4017	0.4315	0.00	0.9442	0.7841	0.1799	0.4315	1.1366	19.00	<,0001
Year	2006	0.1763	0.4997	−0.8031	1.1557	0.12	0.7243	0.1368	0.2284	−0.3109	0.5844	0.36	0.5493	−0.0174	0.2174	−0.4435	0.4087	0.01	0.9362	−0.1406	0.1907	−0.5144	0.2333	0.54	0.4611
Year	2007	1.2457	0.4842	0.2967	2.1948	6.62	0.0101	0.2039	0.2228	−0.2327	0.6405	0.84	0.3601	1.1825	0.2097	0.7714	1.5935	31.79	<,0001	0.3454	0.1837	−0.0147	0.7054	3.53	0.0601
Year	2008	0.8620	0.4966	−0.1112	1.8353	3.01	0.0826	0.5231	0.2276	0.0770	0.9692	5.28	0.0215	0.5849	0.2140	0.1655	1.0044	7.47	0.0063	0.5195	0.1866	0.1538	0.8852	7.75	0.0054
Year	2009	−0.2615	0.5002	−1.2419	0.7189	0.27	0.6011	0.3050	0.2230	−0.1321	0.7421	1.87	0.1714	0.3088	0.2109	−0.1045	0.7221	2.14	0.1431	0.1893	0.1880	−0.1792	0.5577	1.01	0.3140
Year	2010	−0.5025	0.5242	−1.5300	0.5249	0.92	0.3377	−0.5842	0.2333	−1.0414	−0.1270	6.27	0.0123	0.6323	0.2238	0.1935	1.0710	7.98	0.0047	0.0943	0.1861	−0.2704	0.4589	0.26	0.6123
Year	2011	0.0587	0.5014	−0.9240	1.0414	0.01	0.9068	−0.4109	0.2323	−0.8661	0.0444	3.13	0.0769	−0.7875	0.2238	−1.2262	−0.3489	12.38	0.0004	−1.3631	0.1923	−1.7400	−0.9862	50.24	<,0001
Year	2012	0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000		
Quarter	1	−1.6659	0.1512	−1.9623	−1.3695	121.33	<,0001	0.1994	0.0921	0.0189	0.3798	4.69	0.0303	−0.1920	0.0889	−0.3662	−0.0178	4.67	0.0307	−0.8711	0.0740	−1.0160	−0.7261	138.66	<,0001
Quarter	4	0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000		
sd	24	−0.3918	0.3177	−1.0144	0.2309	1.52	0.2175	−0.0100	0.1584	−0.3205	0.3006	0.00	0.9498	2.3499	0.1641	2.0283	2.6715	205.12	<,0001	1.0060	0.1311	0.7490	1.2630	58.86	<,0001
sd	25	0.7790	0.2792	0.2318	1.3263	7.79	0.0053	0.1033	0.1474	−0.1855	0.3922	0.49	0.4832	0.7910	0.1417	0.5134	1.0687	31.18	<,0001	−0.0656	0.1198	−0.3004	0.1691	0.30	0.5836
sd	26	0.1066	0.2892	−0.4603	0.6734	0.14	0.7125	−0.8588	0.1420	−1.1370	−0.5806	36.60	<,0001	0.0851	0.1400	−0.1893	0.3595	0.37	0.5433	−0.6767	0.1193	−0.9105	−0.4428	32.17	<,0001
sd	27	−0.4350	0.4905	−1.3963	0.5263	0.79	0.3751	−1.1407	0.2308	−1.5930	−0.6883	24.42	<,0001	−1.6117	0.2407	−2.0835	−1.1399	44.83	<,0001	−1.3705	0.1873	−1.7377	−1.0034	53.52	<,0001
sd	28	0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000		
Depth	30	0.8852	0.2766	0.3430	1.4274	10.24	0.0014	0.8060	0.1447	0.5224	1.0896	31.02	<,0001	1.0065	0.1614	0.6902	1.3228	38.89	<,0001	1.2411	0.1308	0.9848	1.4974	90.08	<,0001
Depth	50	1.0408	0.2508	0.5492	1.5324	17.22	<,0001	1.5299	0.1266	1.2817	1.7781	145.93	<,0001	1.5963	0.1234	1.3544	1.8381	167.36	<,0001	2.1747	0.1099	1.9593	2.3902	391.31	<,0001
Depth	70	0.4152	0.2459	−0.0668	0.8972	2.85	0.0913	1.0815	0.1255	0.8355	1.3276	74.24	<,0001	1.6409	0.1233	1.3991	1.8826	177.03	<,0001	2.1186	0.1082	1.9064	2.3307	383.07	<,0001
Depth	90	0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000		
s50cpue1	3	−1.5803	0.2599	−2.0896	−1.0709	36.98	<,0001	−1.7274	0.1409	−2.0036	−1.4512	150.30	<,0001	−1.4568	0.1394	−1.7300	−1.1835	109.18	<,0001	−2.5668	0.1179	−2.7979	−2.3357	473.75	<,0001
s50cpue1	12	−0.5397	0.2520	−1.0337	−0.0458	4.59	0.0322	−0.7981	0.1489	−1.0900	−0.5062	28.71	<,0001	−0.8068	0.1400	−1.0813	−0.5324	33.20	<,0001	−1.3838	0.1184	−1.6159	−1.1517	136.51	<,0001
s50cpue1	60	−0.4254	0.1992	−0.8159	−0.0350	4.56	0.0327	−0.3339	0.1146	−0.5585	−0.1093	8.49	0.0036	−0.4038	0.1085	−0.6164	−0.1911	13.85	0.0002	−0.6186	0.0954	−0.8057	−0.4315	42.00	<,0001
s50cpue1	150	−0.1278	0.2209	−0.5607	0.3051	0.33	0.5629	−0.0360	0.1352	−0.3011	0.2290	0.07	0.7899	−0.1476	0.1272	−0.3969	0.1016	1.35	0.2457	−0.1708	0.1119	−0.3902	0.0486	2.33	0.1272
s50cpue1	250	0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000			0.0000	0.0000	0.0000	0.0000		

Table 3. Cont.

Statistic	Estimate	SE	Wald 95% Confidence Limits		Wald Chi-Sq	Wald Pr>ChiSq	Estimate	SE	Wald 95% Confidence Limits		Wald Chi-Sq	Wald Pr>ChiSq	Estimate	SE	Wald 95% Confidence Limits		Wald Chi-Sq	Wald Pr>ChiSq
Length Group	3 cm	3 cm	3 cm	3 cm	3 cm	3 cm	8 cm	8 cm	8 cm	8 cm	8 cm	8 cm	13 cm	13 cm	13 cm	13 cm	13 cm	13 cm	18 cm	18 cm	18 cm	18 cm
Dispersion	12.0331	0.8721	10.3238	13.7424			5.6308	0.1653	5.3069	5.9547			5.0507	0.1361	4.7839	5.3175			4.0717	0.0955	3.8845	4.2590		
	Wald Statistics for Type 3 Analysis of Model						Wald Statistics for Type 3 Analysis of Model						Wald Statistics for Type 3 Analysis of Model						Wald Statistics for Type 3 Analysis of Model					
Year					68.96	<,0001					242.79	<,0001					386.50	<,0001					343.50	<,0001
Quarter					121.33	<,0001					4.69	0.0303					4.67	0.0307					138.66	<,0001
sd					42.62	<,0001					113.24	<,0001					387.00	<,0001					270.45	<,0001
Depth					21.58	<,0001					157.62	<,0001					208.55	<,0001					501.78	<,0001
s50cpue1					40.59	<,0001					185.48	<,0001					121.65	<,0001					579.13	<,0001

Results of density and distribution patterns are shown from several model runs of catch rates for each of the juvenile cod length groups: 0–5 cm (incl. 5 cm): len = 3, 5–10 cm: len = 8, 10–15 cm: len = 13, 15–20 cm: len = 18, i.e. 3–20 cm juvenile cod. Model statistics are given with standard error estimated according to the model estimates, and the Type3 contrast is used for each run. (See also Table S2 in File S1).

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with the model class-level variables including the year, quarter of the year, area (ICES SD), seabed depth and the density of larger cod, above 30 cm in length, as potential predators on juveniles, while the model intercept is α. Runs were performed for each individual length group (L) because the model assumes independence between observations, whereas observations for individual length groups are not mutually independent. Plots of residuals versus model-predicted values were produced for each run, and the goodness of fit was checked by comparing the deviance of the full model with the deviance of a version of the model in which the class variables were excluded, i.e., only testing the intercept of the model. The applied GLMs describe the variability in the CPUE data relatively well when considering that binomial models are either fit to 1 or 0, i.e., integers. The models converged, and no trends were observed in the plots of residuals versus model-predicted values. The significant patterns detected in the cod distribution correspond well to previously reported year, quarter, area, and depth variability data found in the literature (e.g., [22,3,7]).

The model covers all of the years in the period from 2001–2012, and the seasons tested in the model are the 1st and 4th quarter of the year, following the BITS coverage.

The model stratification according to area was based on the ICES subdivisions (Fig. 1), covering SDs 24, 25, 26, 27, 28 and 29.

The model stratification according to different habitats with different seabed depths covered depths of 0–40 m (incl. 40 m): depth = 30; 40–60 m: depth = 50; 60–80 m: depth = 70; 80–100 m: depth = 90; and >100 m: depth = 110, following the depth stratification used in the BITS survey. A comparative testing was made with an alternative seabed depth stratification using two strata: below and above a 60 m depth.

For a reduced number of observations in the BITS data, where hydrographic data associated with the cod CPUE data were available from the ICES DATRAS database (www.ices.dk; 2003–12), the cod density as a function of the bottom temperature and salinity was tested. Here, the bottom temperature class variable was stratified in 5°C intervals, and the bottom salinity was separated into two classes: Below and above 15 psu (Table S2 in File S1). In this analysis, the bottom depth class variable was omitted, since the bottom hydrographic class variables are correlated with depth.

Analyses of juvenile cod intraspecific density patterns

The above model (Eq. 2) was also used to investigate how the juvenile cod density patterns depend on the density of co-occurring larger cod, as potential predators on juvenile cod (cannibalism). Here, the mean density of larger cod (>30 cm) was included in the model as an independent variable (s50cpue1) to test for this effect. The density classes employed in this analysis were as follows: 3 (0–5 individuals/haul), 12 (5–20 individuals/haul), 60 (20–100 individuals/haul), 150 (100–200 individuals/haul), and 250 (>200 individuals/haul).

Furthermore, the yearly density patterns for the smallest juvenile cod plotted from the above model as well as the overall yearly distribution area and patterns of the juvenile cod cohorts obtained using the LGCP method (see section below) were compared to the year class strengths of the individual cohorts from 2001–2010. In Table 2, the year class strengths and recruitment of eastern Baltic cod, as estimated by the ICES WGBFAS assessment working group [7] and through BITS indices from the ICES DATRAS database (www.ices.dk), are presented, together with associated information on major North Sea water inflow events in the Baltic Sea basins during the same period according to previous authors [13,48,49,15,50] and http://www.smhi.se/en/News-

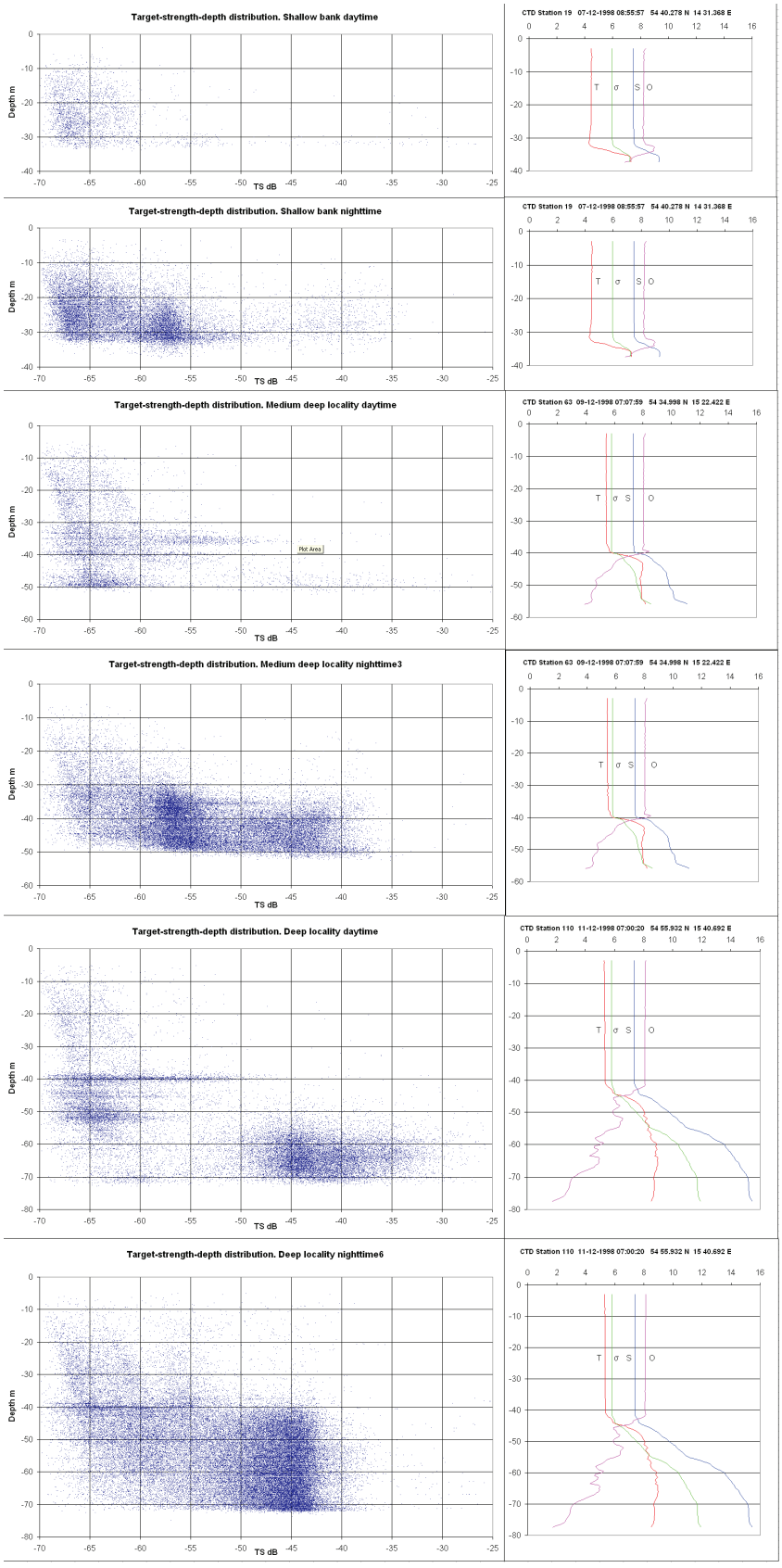
Target-strength-depth distribution. Shallow bank daytime
CTD Station 19 07-12-1998 08:55:57 54 40.278 N 14 31.368 E
Target-strength-depth distribution. Shallow bank nighttime
CTD Station 19 07-12-1998 08:55:57 54 40.278 N 14 31.368 E
Target-strength-depth distribution. Medium deep locality daytime
CTD Station 63 09-12-1998 07:07:59 54 34.998 N 15 22.422 E
Target-strength-depth distribution. Medium deep locality nighttime3
CTD Station 63 09-12-1998 07:07:59 54 34.998 N 15 22.422 E
Target-strength-depth distribution. Deep locality daytime
CTD Station 110 11-12-1998 07:00:20 54 55.932 N 15 40.692 E
Target-strength-depth distribution. Deep locality nighttime6
CTD Station 110 11-12-1998 07:00:20 54 55.932 N 15 40.692 E
Depth m
TS dB
T σ S O

Figure 3. Combined observed TS distributions over 2 full nights and 2 full days continuous recording at each type of locality according to depth, diurnal time, and vertical hydrographical frontal zones as recorded with CTD, i.e. vertical water layer stratification at the 3 types of localities.
doi:10.1371/journal.pone.0070668.g003

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Analysing vertical zoning in hydroacoustic and hydrographic data from specialised surveys

Typical distributions of single targets as a function of depth and TS related to vertical hydrographic frontal zones, i.e., water layer stratification recorded with the CTD, at the 3 types of localities are presented in Figure 3. These distributions cover 2 days and 2 nights of continuous acoustic recording at each locality. They are compared to the calculated TS distributions summarised from trawl CPUE data for cod, herring and sprat from these localities from night or day, as plotted in Figure 4. Here, the TS distributions were calculated from the observed (trawl-caught) species-specific length (L) distributions at the same stations using the following TS-length algorithms:

Juvenile cod <15 cm: $TS = 27\log_{10}L\text{-}76.0$ dB [52,53];
Cod ≥ 15 cm: $TS = 20\log_{10}L\text{-}67.5$ dB [21];
Sprat and herring: $TS = 20\log_{10}L\text{-}71.2$ dB [21,41]

Cod distribution and density patterns based on the LGCP model

The distribution and density patterns of the juvenile Baltic cod cohorts, the 0-group, in autumn and the early 1-group in the following spring, are shown in animated abundance maps for the years 2001–2011 calculated from the LGCP model with parameters obtained by correlation analysis of BITS data. This model makes unbiased estimates of fish abundances by time and space for 0-groups [34], but in contrast to most survey abundance models, which assume the numbers caught in one haul to be independent

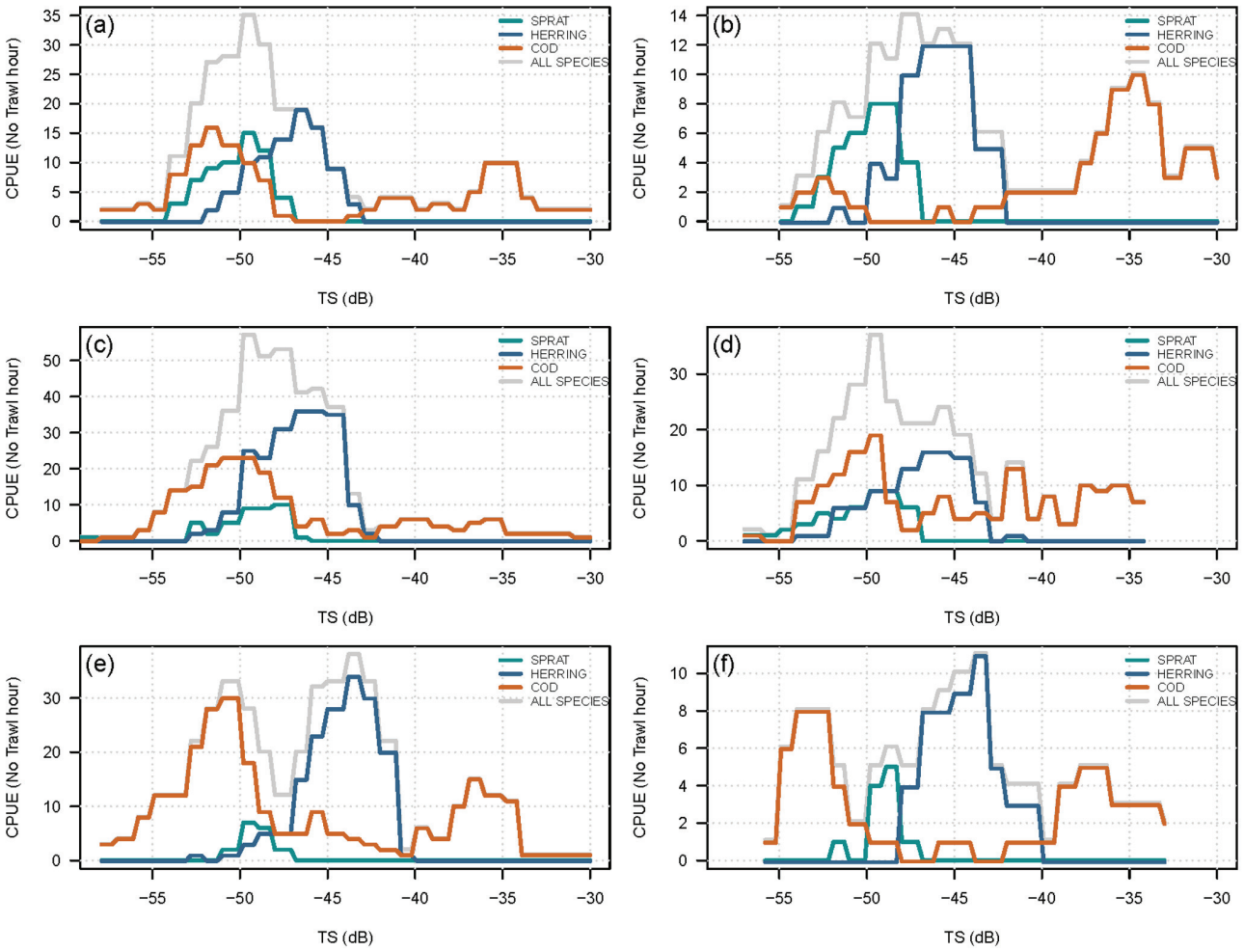

Figure 4. Trawl CPUE of cod, herring and sprat from the special investigated types of localities (Table 1, Fig. 2) during the 1998 specialized surveying according to bottom depth and time of day by length group re-calculated to target strength (TS) distributions. The TS distributions are estimated from observed species specific length distributions in trawl catches at the same stations using the juvenile cod TS-length algorithms from Nielsen and Lundgren (1999) and the clupeoid TS-length algorithm from ICES [8].
doi:10.1371/journal.pone.0070668.g004

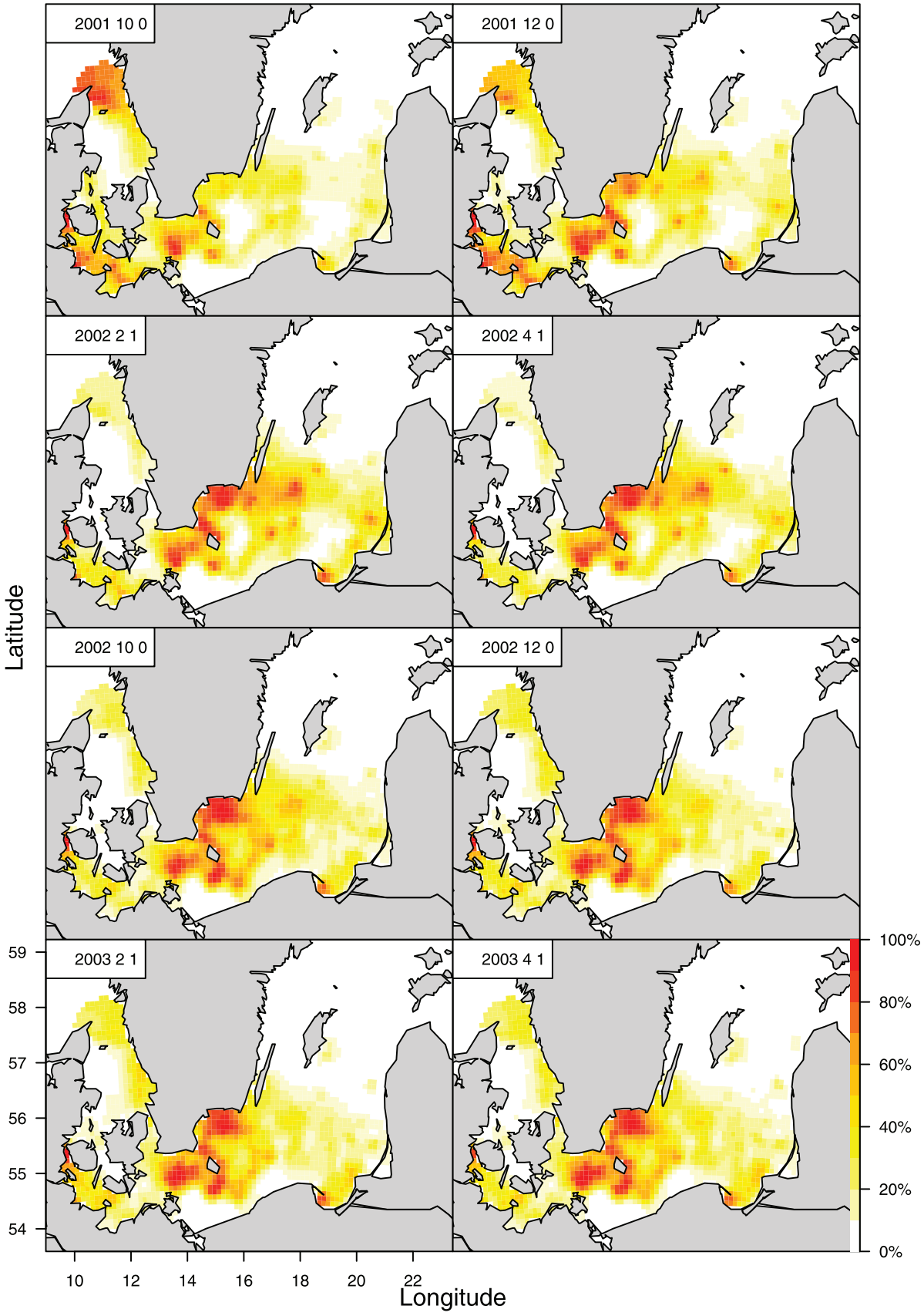
2001 10 0
2001 12 0
2002 2 1
2002 4 1
2002 10 0
2002 12 0
2003 2 1
2003 4 1
Latitude
59
58
57
56
55
54
10
12
14
16
18
20
22
Longitude
100%
80%
60%
40%
20%
0%

Figure 5. Distribution and density patterns in form of abundance maps of juvenile cod cohorts as 0-group in the autumn and early 1-group in the following spring where 0-group cod in year Y is correlated with 1-group in year Y+1. The abundance maps are estimated from correlation analysis with the LGCP statistical co-variance model (Eq. 3) of BITS data (DATRAS exchange format) for the cohorts 2001–2002.
doi:10.1371/journal.pone.0070668.g005

of the numbers caught in all other hauls, the LGCP model utilises the positive correlation between the numbers of fish caught when the spatial distance between the hauls decrease. The current model is modified to follow individual cohorts, where the 0-group cod in year Y are correlated with the 1-group in year Y+1. It is advantageous to follow the cohort distribution and movement of the late-spawned 0-group into the next year as the early 1-group to avoid the assumptions about growth rates that would be made for early- and late-spawned juvenile cod, respectively, if only length groups were followed assuming a natural length-based correlation. Hence, the model estimates spatial and seasonal correlations assuming Poisson-distributed observations and multivariate log-normal means, including zero observations and over-dispersion, a spatiotemporal correlation structure and potential correlation between different cohorts. Accordingly, the LGCP model estimates the density $\gamma(\Delta x,\Delta a)$ with the co-variance model as follows (Eq. 3):

$$\gamma(\Delta x,\Delta a)=\sigma^2\rho^1(\Delta x)\rho^2(\Delta a)+\sigma_n^2 1_{(\Delta x=0,\Delta a=0)} \qquad (3)$$

where a is the fractional cohort age (e.g., for the 2001 year class caught in month 2 of 2002, a = 1.167 years); $\rho^2(\Delta a)$ is the age correlation at a separation of Δa; x is the position (spatial); $\rho^1(\Delta x)$ is the spatial correlation at a distance of Δx; σ^2 is a variance parameter for large-scale variation; and $\sigma_n^2 1_{(\Delta x=0,\Delta a=0)}$ is the variance for small-scale variation. Samples of highly disaggregated spatial and seasonal gridded maps (3*3 nautical miles, per month) are shown in Figures 5, 6 and 7 (and Figs. S1, S2), as estimated from spatial, seasonal and intra-cohort age correlations in the BITS observations. The LGCP model fits the data and converges well, with a high intraspecific time and spatial correlation, when it is parameterised using the maximum likelihood method and the Laplace approximation, where the maxima and uncertainty can be estimated from the positive definite Hessian matrices in which all rows are independent.

Ethics statement

No humans or primates or laboratory animals have been involved in the study. There has been no sampling from private land, and the field studies did not involve endangered or protected species. Only fish sampled in public sea areas have been used. All fish have been sampled with research survey trawls under or related to ICES (International Council for Exploration of the Sea; www.ices.dk) coordinated international standard trawl and hydroacoustic surveying. The sampling and handling of fish follows strictly all ICES guidelines, procedures, legislative rules, and permissions from national governments for sampling and handling of fish in fisheries research surveys. The sampling was conducted by national government owned research vessels following Danish national legislation, permissions, and ethics for handling of wild caught fish. The sampling has been performed under repeated international standardized surveying where the research vessels have full permission to sample from all relevant national public authorities (governments) in the Baltic waters.

Results

Influence of geographical area and topography (H01 and H02)

The results of the GLM (Table 3) applied to the BITS CPUE data show that the highest densities of the smallest juveniles (0–5 cm) are found in SD25, followed by SD26, corresponding to known spawning areas in the Bornholm Basin and Gdansk Deep. Lowest densities are observed in SD24 and SD27. However, juvenile cod exhibit an increasing density with increasing size in SD24 (Arkona Basin), and for the sizes of 10 cm and larger the highest densities occur in this area. The highest seasonal density of the smallest cod is found in the 4th quarter (Table 3), but they appear only seldom at that time in SD29, while always observed in all areas in the 1st quarter (latter results not shown). Also, juveniles of the 5–10 cm length group are found with the highest densities in SD25, but then followed by SD24 and SD28 (Gotland Basin). In general for all size groups the densities are low in SD27 during 2001–2012. No major seasonal density differences could be detected for the larger size groups, with the exception of the 15–20-cm group showing the (statistically significant) highest density in the 1st quarter.

The above significant patterns in the geographical distribution of nursery grounds are also observed in the high-resolution density patterns resulting from the statistical LGCP model applied to the individual 2001–2010 cod cohorts. (Figs. 5, 6, 7; Figs. S1, S2). Even as small, 0-group juveniles in Oct.–Dec. the cod shows a widespread geographical distribution area in the CBS, ranging from SD22 to SD28. The distribution of this group is generally scattered but also presents high-density concentrations in the central Baltic basins. The main concentrations are found in the Arkona, Bornholm, Gotland, and Gdansk Basins and in the more coastal Hanö Bay (Fig. 1). The same wide distribution and concentrations are estimated for the early 1-group in Feb.–Apr. by the LGCP model; i.e., the modelling indicates a high consistency in the distribution patterns for different seasons and juvenile life stages. However, variation is observed in the extension of the distributions between years, where both the 0- and 1-groups show a very northerly distribution in the later years (2007–2010 cohorts), up into the north and east of Gotland and along the western coasts of Poland, Lithuania, Latvia, and Estonia, which is not observed for the early period cohorts.

Influence of water layers and seabed depth (H03 and H02)

Juvenile cod were caught at localities with bottom depths ranging from 16 m to more than 100 m, though they occur with a relatively low density at bottom depths deeper than 80 m.

The vertical distributions of juvenile cod found in the specialised surveys were near-bottom and pycnocline-associated (Figs. 3–4). No juvenile cod with sizes of 2–3 cm or larger were caught in the upper and middle pelagic water layers above the pycnocline with any of the small trawl gears used (Table 1; 0 values not shown); i.e., these size classes were not found in V-shaped, double oblique hauls only covering the surface and mid-water layers. Juvenile cod of lengths 3 cm and larger were all trawl caught in the near-pycnocline and seabed layers in bottom hauls, during both day

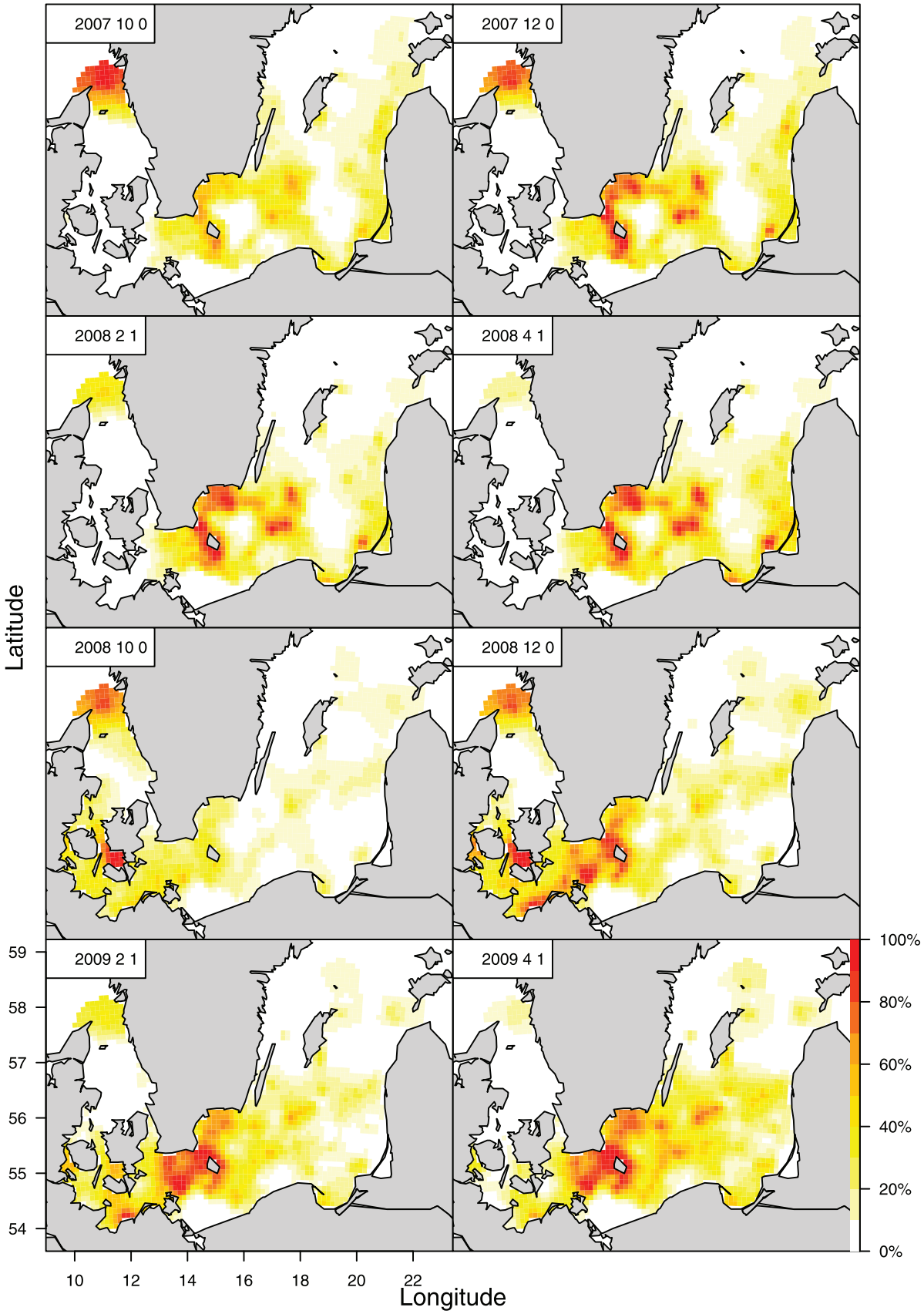

Figure 6. Same as Figure 5, but for the juvenile cohorts 2007–2008.
doi:10.1371/journal.pone.0070668.g006

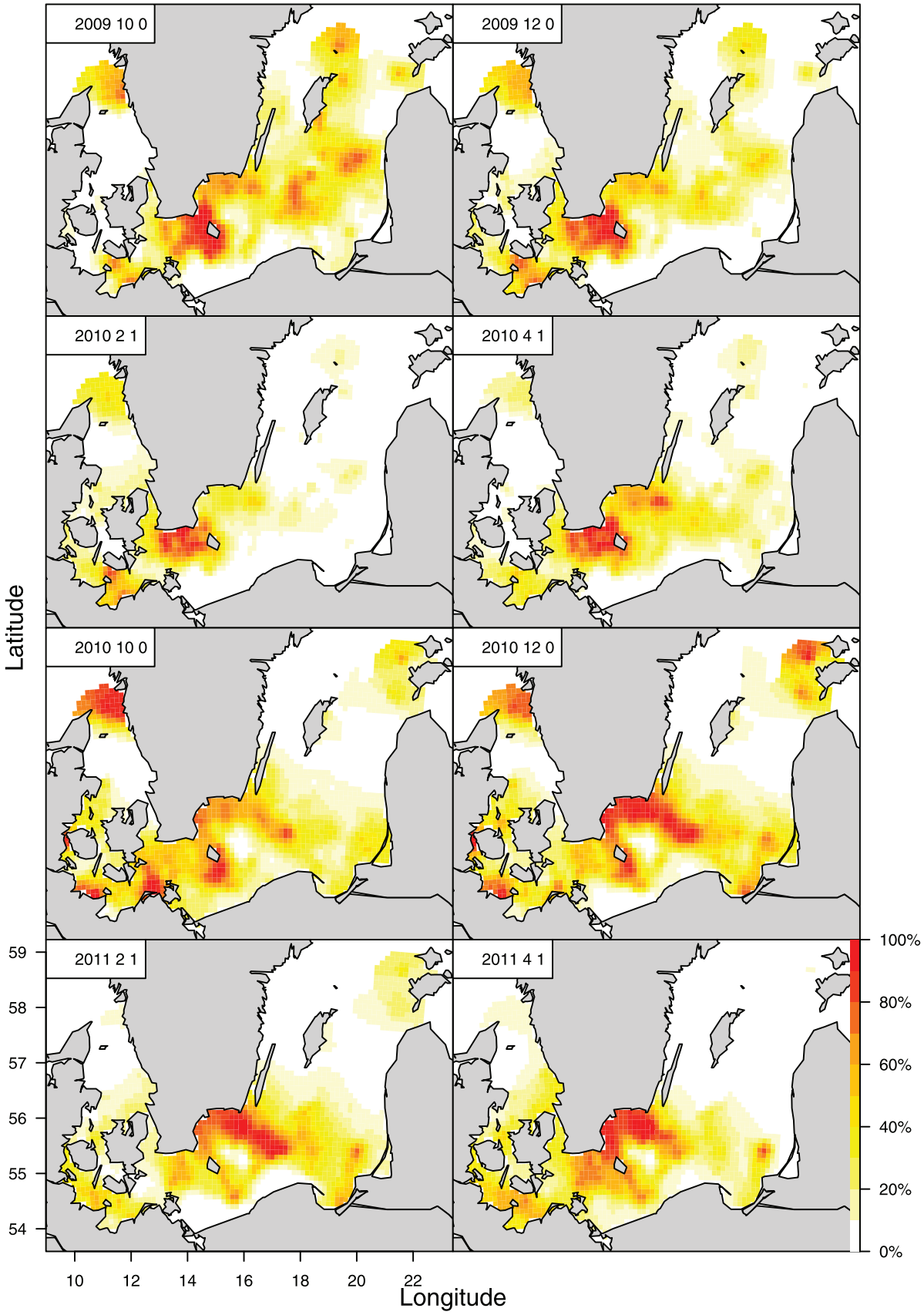

Figure 7. Same as Figure 5 but for the juvenile cod cohorts 2009–2010.
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and night (Figs. 3–4), indicating a constant, rather demersal distribution for these life stages. These findings further indicate that settling occurs at a length of approximately 2–3 cm for the central Baltic juvenile cod.

Regarding the interpretation of the vertical TS distributions shown in Figure 3, TS estimates from the literature must be used. Juvenile cod, sprat and small herring exhibit TS values within the same range (Figs. 3, 4; [25]). Nielsen and Lundgren [52] found TS values ranging from −59.8 to −44.8 dB for 0-group cod in the size range of 75–98 mm and from −57.1 to −37.0 dB in the size range of 159–188 mm (North Sea salinities). Nakken and Olsen [54] reported TS values between −50 dB and −47 dB for fixed, anaesthetised juvenile cod in the size group between 7 and 9 cm. Ona [55] estimated a mean TS of −57.1 dB, with a distribution ranging from −69 dB to −48 dB during night time in a rearing pond for juvenile cod in the size class of 3–8 cm (mean length, 5.1 cm). Accordingly, cod in the size range of 3–15 cm mainly show a TS distribution ranging from −60 dB to −45 dB, consistent with Figure 4. Numerous targets and dense layers of mysids were easily detectable and distinct in the hydroacoustic 38 kHz split beam profiles, especially during night time. The plankton species composition in different water layers was investigated via depth-stratified fishery sampling using BONGO and MIK ring trawls during the specialised surveys, which showed dense aggregations of mysids, with the dominant species being *Mysis mixta* [56,57]. The detected mysids were up to 20 mm in length, and the expected TS values for mysids range from approximately −75 to −65 dB based on the literature [58]. Targets within the range −70 to −65 dB were typically found to be abundant in vertical layers from the sea surface to under the pycnocline (Fig. 3). At localities with well-mixed waters, these targets are more evenly scattered throughout the entire water column. The captured juvenile cod show a TS distribution between −60 and −45 dB (Fig. 3). For this TS range, distinct vertical patterns in the obtained TS distributions and numbers of single fish targets tracked can be observed in the profiles from the three different types of localities, with distinct hydrographic characteristics (Fig. 3). Based on the findings for trawl caught cod and the corresponding fish TS distributions (Figs. 3–4), it appears that in shallow-water bank areas with bottom depths of approximately 40 m, the small-to-medium-sized targets show a more even distribution in the water column starting above the pycnocline (35 m depth) and extending up to a depth of 10 m (Figs. 3–4), while the larger targets of cod and herring are distributed just above the pycnocline, both during night and day. At the intermediate depth localities (60 m) and in the deep basin areas (80 m), the small-to-medium-sized juvenile cod TS is mainly distributed in the pycnocline, where there is extensive stratification related to oxygen, salinity, and temperature, being located around the 30–50 m depth layer in the intermediate depth areas and around the 40–70 m layer in deep sea areas (Figs. 3–4). At deep localities, the density of the water layer below the pycnocline is relatively high. The near-bottom oxygen concentrations vary from near saturation at localities with well-mixed water, showing a continuous decline in the water column beginning at the oxycline at localities with stratified water layers, to very low concentrations (0–1 $ml.l^{-1}$ O_2) close to the seabed at deep localities. At all types of localities investigated, no targets were detected in the oxygen-depleted layers from the seabed to 5–7 m above the seabed, which corresponded to oxygen concentrations below 7 $ml.l^{-1}$ O_2 in the shallow bank areas, below 4 $ml.l^{-1}$ O_2 in the intermediate depth localities, and below 2 $ml.l^{-1}$ O_2 in the deep basin areas. However, in the deep sea basin areas, most of the targets, including juvenile Baltic cod, were observed in water layers with oxygen concentrations between 2 and 4 ml $O_2.l^{-1}$, regardless of the size group.

Distinct diurnal patterns could be observed in the distribution of the acoustic targets, including those corresponding to juvenile Baltic cod (Figs. 3–4), with the smallest juveniles being found at deep, intermediate depth and shallow localities at both day and night, but with the highest catch rates occurring during night at the intermediate depth and deep localities. Single targets in the TS range of juvenile cod appear to be concentrated during night time in and below the pycnocline, compared to a more scattered distribution during the day, extending well above the pycnocline.

The results of the GLM (Table 3) show distinct trends in the vertical distributions and density patterns of the juvenile cod according to bottom depth stratification. For the smallest juveniles, with lengths of 0–5 cm, the densities are higher at localities with bottom depths of 40–60 m than in shallow areas (0–40 m bottom depth), and the densities decrease significantly with increasing bottom depths from 60 m for this size group. For the larger, 5–10 cm and 10–20 cm juveniles, the highest densities are also observed at localities with a depth of 40–60 m, followed by those with 60–80 m, but with lower densities being recorded in shallow areas (0–40 m depth) for the largest juveniles (10–20 cm). All size groups (0–20 cm) of juvenile cod are found in the deepest areas, with bottom depths greater than 80 m, but with significantly lower density here. In the 4th quarter of the year, the smaller juveniles occur more frequently at depths greater than 80 m compared to the 1st quarter, and in general, juvenile cod are seldom found at localities with bottom depths greater than 100 m (not shown). Accordingly, as the juveniles become larger, there is a tendency toward their densities increasing in the deeper habitats and localities. No differences in density were found due to the near-bottom salinity, but significantly lower densities were observed in bottom waters with a temperature of less than 5°C compared to the 5–10°C and above 10°C temperature strata. This appears to be a generally consistent and significant pattern for all juvenile cod size groups (Table S2 in File S1).

Influence of year class strength and intraspecific density (H04)

The GLM results show significant variations in the juvenile cod density between the different study years. For the smallest, 0–5 cm juveniles (mainly the 0-group), the highest densities are found in the years 2001, 2003, 2004, 2007, and 2008, and intermediate densities are observed in 2006, while the lowest densities are found in 2002 and from 2009–2012. The densities recorded in 2003, 2004, and 2007 are significantly higher than in 2012, and the highest densities occur in 2004 and 2007. In late spring of 2003, there was a strong inflow to the Baltic, resulting in favourable hydrographic conditions for spawning and cod fry survival; however, the density of the smallest cod was not found to be higher at this time than in the other high-density years, even though the peak spawning period of the eastern Baltic cod stock is during summer [59,60]. A similar pattern of high densities in 2001, 2003, 2004, and parts of 2007 and 2008 and generally lower densities in the most recent period, from 2009–2011, is observed for larger juveniles, in the 5–10 cm, 10–15 cm and 15–20 cm length groups. Peak densities are observed in 2004 for the larger cod, extending into 2005 for the largest juveniles, which may correspond to the 2003 cohort.

Distinct intraspecific density dependence is indicated by the results from the GLM (Table 3). For all of the length groups of juveniles investigated, there is a significant increase in density associated with an increasing density of large cod with sizes above 30 cm, which most likely means that juveniles and larger cod

aggregate in habitats that are favourable or attractive for both groups.

The geographical distribution and density patterns of the juvenile cod vary with the year class strength for eastern Baltic cod. The year classes formed in 1976, 1977, and 1980 were strong due to favourable conditions for reproduction in the spawning areas in the southern and central Baltic Sea [7], which resulted in the highest historical levels of SSB being observed in 1982–1983. These conditions were associated with frequent inflows of oxygenated, saline water from the North Sea. During the period investigated in the present study, from 2001–2011, the 2003, 2006, 2007, 2008, 2009, and 2010 year classes were relatively strong according to the ICES WGBFAS assessment [7], which was partly confirmed by the ICES DATRAS indices (www.ices.dk) for the 2003, 2006, and 2007 year classes (Table 2). In the same period, strong inflow events into the Baltic were only recorded in spring 2003 and autumn 2011 (Table 2). There was a strong year class associated with the 2003 inflow, but other year classes were also relatively strong, even when no major inflow was observed. Overall, there was not complete consistency in the overlap between the years with the highest densities of the smallest juveniles (2001, 2003, 2004, 2007, and 2008 and, to a lesser extent, 2006) and the years with estimated high recruitment (2003, 2006, 2007, 2008, 2009, and 2010). However, given the annual variability in the overall distribution between years observed from LGCP modelling, it is clear that in more recent years, when there have been more frequent relatively strong year classes of eastern Baltic cod (Table 2; [7]), a tendency towards a north-eastward extension of the distribution area for the 2007–10 cohorts of both 0- and 1-group juveniles can be observed.

Discussion

Horizontal and vertical distribution and density patterns (H01 and H03)

The distribution and density patterns of juvenile cod have been described in the scientific literature for several sea and coastal water areas, such as the NE and NW North Atlantic (e.g., [61,62,63,64,65,66,67]) and the North Sea (e.g., [68,69]). However, the distribution patterns of juvenile Baltic cod have only been described theoretically via hydrodynamic modelling, with only limited comparisons being made with survey data and fishery observations (e.g., [22,3]). In contrast, vertical and horizontal distribution patterns have been investigated for larger, mature and spawning cod based on hydroacoustic surveys ([59,60].

It appears from the present GLM analyses, that the smallest juvenile Baltic cod (0–5 cm) occur with the highest densities within the known spawning areas in the Bornholm Basin (SD25), Gdansk Deep (SD26) and parts of the Gotland Basin (SD28), while larger juveniles show the highest densities in more westerly areas in the Arkona Basin (SD24), followed by the Bornholm Basin (SD25). The smallest size group is mainly observed during the 4th quarter, corresponding to individuals from the late summer peak spawning period of eastern Baltic cod (SD25, SD26, SD28) [70,71]. The increasing density associated with increasing size in SD24 could indicate migration between areas, where Eero *et al.* [29] also found indications of the migration of small cod from SD25 to SD24 in later years. Survey trawl gear selectivity associated with differences in the spawning seasons and growth of eastern and western Baltic cod could influence the survey catchability of the smallest juveniles (<2 cn); e.g., the juveniles in SD24 might have grown to a larger size class before being caught in the 4th quarter survey. However, given the early spawning of western Baltic cod in the spring, the smallest juveniles would most likely have been observed in at least small numbers in the 1st quarter surveys in SD24 if they were abundant here. Moreover, catchability effects do not influence the finding that there is a consistently higher density of the larger size groups in westerly areas. The applied LGCP statistical modelling confirmed these overall geographical distribution patterns on a high resolution scale in time and space. Here, it should be noted that the LGCP results are not influenced by gear selectivity to the same extent as the GLM results because the LGCP model adjusts the mean quarterly CPUE values of the cohorts according to the correlations between the quarterly observations. It appears that late 0-group and early 1-group cod are widely distributed throughout the CBS, with the highest concentrations being observed in the basins and the more coastal area of Hanö Bay, which is consistent over seasons for the cohorts. The annual variability shows a clear tendency towards a north-eastward extension of the distribution areas in the more recent years of the investigated period (2007–2010 cohorts). This may be associated with a more frequent occurrence of relatively strong eastern Baltic cod year classes. Consequently, even though the juvenile cod consistently show the highest concentrations in the Baltic basins, without considerable yearly and seasonal variation by age being detected, they are still widely distributed, and the extent of their distribution varies by year; i.e., they do not exhibit geographically limited nursery areas.

Concerning the vertical distribution, the GLM revealed an increasing juvenile cod density associated with bottom depth as the fish become bigger. The main nursery areas for the smallest juveniles are found at bottom depths down to 60 m, with peak densities occurring at 40–60 m, while larger juveniles show the highest densities at depths of 50 to 80 m. However, all size groups are found at localities with bottom depths of greater than 80 m (down to 100 m), but at lower densities, which is consistent with the wide distribution described above. The hydrographic conditions, especially the oxygen concentrations, in the near-bottom water layers appear to have a significant influence on the juvenile Baltic cod distribution and density patterns based on comparison with the results from the integrated trawl and acoustic specialised surveys. Indeed, juvenile cod show the highest abundance in well-oxygenated waters and in waters warmer than 5°C, but they also occur at deeper localities with oxygen-depleted waters, and a great deal of variability is observed between years. Even the smallest size group of juvenile cod is found at deep localities with oxygen-depleted waters, where the bottom oxygen concentrations can fall to 2 ml.l^{-1} O_2 (or even lower). Juvenile cod are found both at stratified and well-mixed localities and at localities where the distance between the pycnocline and the bottom is rather high. However, at the stratified localities, there is a relatively lower density observed in the near-bottom water layers with oxygen O_2 concentrations <2 ml.l^{-1}. The choice of this reference tolerance limit for testing the occurrence of juvenile Baltic cod is supported by the limits of approximately 2.4 ml.l^{-1} found for cod in the Gulf of St. Lawrence [72] and approximately 3 ml.l^{-1} reported for adult cod in the CBS by Tomkiewiez *et al.* [59]. Similar oxygen tolerance levels for Atlantic cod have been documented by Plante *et al.* [12] and Chabot and Dutil [11], and physiological experiments examining gas secretion and resorption in the swimbladder of juvenile cod related to vertical migration carried out by Harden Jones and Scholes [73] indicate that extensive, long-range diurnal vertical migrations of juvenile cod are possible. Neuenfeldt e*t al.* [13] found that adult Baltic cod could remain for several hours in hypoxic waters showing less than 50% oxygen saturation to forage. We observed that juvenile cod occur in relatively low numbers in the nearest-bottom water layers (up to 5–7 m above seabed), according to the acoustic single-target

distributions recorded in both day and night; however, the exact location from the seabed up to approximately 6 m cannot be determined from the trawl fishery sampling conducted here, taking the trawl gaps into account.

The characteristic hydrographic feature of the deep central Baltic basins is a permanent halocline separating an intermediate cold water layer from a saline bottom water layer [1,2,13]. Within the deep water and bottom layers (>60 m), oxygen depletion has often been observed, but well-oxygenated water is normally found in the halocline (40–60 m depths) [22]. Simulations of the seasonally averaged drift patterns of cod larvae spawned at different times in the Bornholm Basin from 1986 to 1999 conducted by Hinrichsen *et al.* [22] predict both a northern and southern distribution of settling sites around Bornholm Basin in shallow-water (coastal) areas compared with observed distributions from juvenile pelagic and demersal (BITS) trawl surveys for the period 1993–2000. Here, the densities of juvenile cod were predicted to be highest in southern areas with bottom depths of less than 40 m for early- and late-spawned individuals. A problem in this case is that the settled stages of juvenile cod were not well covered by the BITS survey design for this time period. The results may therefore be flawed due to the different trawl catchability results according to area. Hinrichsen *et al.* [3] conducted the same type of drift model simulation to predict transport patterns for larvae spawned in the three major spawning grounds of the CBS for the period from 1979–2004 to predict potential settling and nursery areas of early juvenile eastern Baltic cod and potential habitats showing a high probability of successful settlement. They concluded that the settling and early nursery areas are situated at the edges of the basin, down to where the halocline meets the bottom, while the probability of settlement in the deeper central parts of the basin is low because of the minimum oxygen requirements for successful settling. This means that settling would only be expected to occur on the northern and southern slopes of Bornholm Basin, the western and eastern slopes of Gotland Basin, the eastern part of the Gdansk Deep, and along the Lithuanian and Latvian coasts, showing both yearly and decadal variability. Concerning oxygen requirements, these authors refer to Chabot and Dutil [11], indicating that environments exhibiting an oxygen saturation below 40% are not suitable for settling, resulting in a reduced probability of successful settlement. Additionally, they refer to the finding that data storage tags indicate that Baltic cod remain in less-oxygenated water masses (<40% oxygen saturation) for feeding purposes only ~10% of the time. Finally, they note that they did not study the importance of swimming ability when examining the drift of virtual larvae and juvenile cod. When Hinrichsen *et al.* [74] modelled the passive drift of simulated cod eggs and larvae originating from Kattegat to the Eastern Baltic Sea Basins over 80–100 days before settling, it was observed that they could be distributed over a long distance in all directions from nearly all spawning sites before settling. Accordingly, the pelagic fry are most likely distributed over a large potential settling area, limited by various factors, as indicated by other studies addressing the optimal and lethal food and oxygen conditions for settling.

In contrast to the predictions from these studies, we observed that 3 cm and larger juvenile cod are widely distributed throughout the CBS, including in deep sea areas with oxygen saturation well below 40%. Consequently, hypothesis H01 is rejected. The settled stages do not occur only in shallower (more oxygen saturated) areas down to 60 m, e.g., at the edges of the Baltic basins, and show limited geographical nursery areas across years. Hypothesis H03 is also rejected, as the settled stages exhibit distinct vertical distribution patterns according to hydrographic vertical stratification. However, despite concentrating in certain layers according to hydrographic factors and frontal zones, these stages show a high tolerance and are also widespread at deep localities with less suitable hydrographic conditions.

Potential schooling behaviour of juvenile Baltic cod (H02)

The investigated settled juvenile Baltic cod do not aggregate in dense schools but show a more scattered distribution over a larger area and within the water column. In the North Sea, cod larvae and pelagic 0-group cod are more abundant and show a better condition at frontal zones than found elsewhere at neighbouring sites [69]. Settled juvenile cod have been found to aggregate at the north-eastern edge of Georges Bank at 70–100 m depth dependent on seabed sediment type and hydrographical features [67]. The concentrations of juveniles can also be expected to be associated with hydrographic frontal zones in the Baltic, and we detected the highest concentrations close to the pycnocline frontal zone. Distinct patterns (patchiness) could be observed in the vertical distribution of single zooplankton targets (most likely mysids), which during night time in the late autumn and early winter, were very similar to the single target distribution observed for juvenile cod at localities with both stratified and well-mixed waters. The juvenile cod distribution can be associated with predation on mysids. Mysids were found in the stomach contents of the captured juvenile cod even at very deep localities, though in smaller relative amounts compared to the fish caught in shallower-water localities, where the juvenile cod were found to be in significantly better condition (not shown). This observation is in accordance with the findings of Patokina and Kalinina [75] and Hüssy *et al.* [76], who reported that Baltic cod smaller than 20 cm distributed in bottom depths as low as 50 m were found to feed mainly on mysids (*Mysis mixta*), while at depths of up to 75 m, benthos (Polychaetes) represented the predominant food source. The distribution of pelagic life stages corresponding to metamorphosed juvenile cod 2 cm long and smaller has not yet been fully mapped. The offshore and coastal waters of the CBS have been surveyed intensively in all areas, in all depths and layers, and during all periods of the year. These surveys have been conducted using a broad variety of small-meshed trawl sampling gears and gill nets, including specially designed young fish trawls and ring nets targeting juvenile life stages, in addition to associated intense hydroacoustic recording, both in specially designed surveys and standard Baltic fish surveys. If the smallest and larger juveniles occur in very dense patches, or in high concentrations in slope areas where the pycnocline meets the seabed, they would have been detected, taking into account the international effort and the combined methods used in the search for these fish during the last 15 years. It appears to be unlikely that the smallest stages of juvenile cod consistently occur in dense patches in the nearest-bottom water layers, outside the reach of the applied trawl gears and acoustic recording apparatuses, as they exclusively feed on pelagic plankton such as copepods (and mysids), and rubber discs that exhibit close seabed contact are used in these trawl survey gears, in addition to the fact that the water layers closest to the seabed are oxygen depleted, making continuous occurrence in these layers unlikely. Accordingly, hypothesis H02, stating that settled juvenile Baltic cod aggregate in dense schools and show schooling behaviour, as observed in the North Sea [68,69], is rejected.

Survey fishing efficiency and selectivity in relation to the observed distribution patterns

The diurnal patterns observed in the juvenile Baltic cod distribution are distinct, especially at deeper localities. Diurnal variation in the juvenile cod distribution has also been described in

other areas, such as the North Sea [77,78,79]. It appears from the present observations of trawl-caught cod and the corresponding fish TS distributions that the smallest juveniles are found both at day and night in deep, intermediate depth and shallow localities, but with the highest catch rates being recorded in the first two types of localities during night. The single targets in the TS range of juvenile Baltic cod appear to concentrate during night time in and below the pycnocline frontal zone, compared to the more scattered distribution detected during day, which extends well above the pycnocline. The higher night time catch rates obtained are in accordance with what has been observed for near-coastal north-western juvenile cod [80]. The greater numbers of night-caught juvenile cod could be due to increased catchability at this time, as the juveniles may not escape through mesh as easily in the dark, when the trawl twines are not visible. However, it is questionable if this makes a difference in the intermediate depth and deep localities, where the intensity of daylight is rather low. The single target TS distributions observed in the acoustic data are not influenced by gear selectivity, and it appears to be evident that night time concentrations are higher. The survey trawl does not catch all juvenile cod. The L50 is not documented for the TV3 trawl, but some of the smallest 0-group cod will escape the trawl, either through the mesh or under the bottom gear. We only caught cod from size groups of 2 cm and larger, and the smallest juveniles were infrequent. Engås and Godø [24] reported escape under the gear footrope (bottom gear) when using bobbin bottom gear, but this is considered to be a minor effect here, as the TV3 trawl has rubber disk bottom gear exhibiting close seabed contact. In the present context, where no absolute abundance estimates of juveniles are used, but the relative density and distribution are analysed, the effects of selectivity and different fishing powers dependent on size are considered unimportant. Although the smallest juveniles were not observed and their distribution and density patterns have not been fully mapped, there is no reason to believe that the fishing power and selectivity in the survey trawls will be different between different years, quarters, areas, or depth strata, thus influencing the results of the present analyses.

Density dependence in relation to cannibalism and year class strength (H04)

The juvenile stages of demersal fish stocks and the year-class strength are thought to be regulated in part through density-dependent processes including competition for limiting food resources and predation [81,63,82]. Cannibalism on juvenile eastern Baltic cod has been documented [26,83,27,28,18,29]. The present analyses of intraspecific density patterns indicate that there is a high degree of overlap between juvenile and larger (>30 cm) Baltic cod. Accordingly, the juveniles and the larger cod aggregate in the same habitats, which are favourable and attractive for both small and larger cod. A potential explanation for this phenomenon is that the larger predators seek the habitats of the juveniles to prey on them. However, this does not appear to be a likely overall strategy for the cod, given that investigations of Baltic cod stomach contents conducted in recent years have not indicated any important cannibalism during the investigated period [17]. Furthermore, LGCP modeling showed a north-eastward extension of the juvenile cod distribution area in years with relatively stronger eastern Baltic cod year classes. Accordingly, hypothesis H04 cannot be rejected based on the present data.

Future studies

Future studies could analyse correlations in the density and distribution patterns of juvenile cod in detail according to the specific distribution patterns of other species such as mysids, sprat and herring, taking into account detailed data on oxygen contents close to the seabed. Here, it is relevant to evaluate the extent of overlap with other potential prey species for larger cod, such as sprat and herring. An obvious tool to be applied in these investigations is LGCP models integrating the correlations between species distributions.

Supporting Information

File S1 Table S1 (containing acoustic echosounder and hydrographical CTD profiler calibration parameters); Table S2 (containing the generalized linear model maximum likelihood parameter estimates of CPUE for the statistical model 1 in Equation 2 modified to only include the dependent variables year, quarter, salinity and temperature.
(DOCX)

Figure S1 Same as Figures 5–7, but for the cohorts 2003–2004.
(EPS)

Figure S2 Same as Figures 5–7, but for the cohorts 2005–2006.
(EPS)

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Author Contributions

Conceived and designed the experiments: JRN BL. Performed the experiments: JRN BL. Analyzed the data: JRN BL KK. Contributed reagents/materials/analysis tools: JRN BL KK FB. Wrote the paper: JRN. Revising the manuscript critically for important intellectual content: JRN BL KK FB. Interpretation of the data: JRN BL. Final approval of the version to be published: JRN.

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A Statistical Model for Estimation of Fish Density Including Correlation in Size, Space, Time and between Species from Research Survey Data

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Abstract

Trawl survey data with high spatial and seasonal coverage were analysed using a variant of the Log Gaussian Cox Process (LGCP) statistical model to estimate unbiased relative fish densities. The model estimates correlations between observations according to time, space, and fish size and includes zero observations and over-dispersion. The model utilises the fact the correlation between numbers of fish caught increases when the distance in space and time between the fish decreases, and the correlation between size groups in a haul increases when the difference in size decreases. Here the model is extended in two ways. Instead of assuming a natural scale size correlation, the model is further developed to allow for a transformed length scale. Furthermore, in the present application, the spatial- and size-dependent correlation between species was included. For cod (*Gadus morhua*) and whiting (*Merlangius merlangus*), a common structured size correlation was fitted, and a separable structure between the time and space-size correlation was found for each species, whereas more complex structures were required to describe the correlation between species (and space-size). The within-species time correlation is strong, whereas the correlations between the species are weaker over time but strong within the year.

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Introduction

A survey design was developed to extend the coverage of the standard ICES (International Council for Exploration of the Sea) Baltic International Trawl Survey (BITS; www.ices.dk) during 2009–2012 in the Western Baltic Sea (WBS). The aim was to enhance the power of the environmental impact assessment on the fish population dynamics of the establishment of the fixed transport link in the Fehmarn Belt area between Denmark and Germany in the WBS (Fig. 1). The resulting survey data with high spatial and seasonal coverage for a range of commercially important fish species are analysed with an extended variant of the Log Gaussian Cox Process (LGCP) statistical model [1,2,3].

Research survey data are often analysed under the assumption that the observations are independent, irrespective of trawl position, and distributed according to either extensions of the lognormal [4] or negative binomial distributions [5,6]. Other studies have presented extensions of the multinomial distribution to account for data dispersion or correlation [7] or have used the geostatistical kriging approach to account for spatial correlations in the observations [8,9]. Kristensen [1] and Lewy and Kristensen [2] estimated North Sea cod distribution patterns with the LGCP model using a statistical approach to determine spatial correlations between observations from surveys according to age. The overall formal structure of this model is given by Kristensen et al. [3]. The LGCP model is one of several models in the general family of parametric geostatistical methods, including hierarchical models and/or Gaussian latent variable models, that describe correlations in different dimensions including spatial correlation [8,10]. An extension of the model was applied to mackerel (*Scombrus scombrus*) larvae survey data [11] based on additional temporal co-variance in spatial distributions.

In the present study, a similar extension of the LGCP model is applied to the standard and extended BITS survey data for Baltic cod and whiting. In contrast to most survey abundance models, which assume that the numbers by size caught in one haul are independent of numbers by size caught in all other hauls, the LGCP model utilises the fact that the correlation between numbers of fish caught increases when the distance in space and time between them in the sea decreases and, similarly, that the correlation between numbers caught of different sizes in a haul increases when the difference in size decreases. The model is further extended in two ways with the following aims. First, instead of assuming that the size correlation is used on the natural length-based scale, the correlation model is developed to allow the length scale to be transformed with, e.g., a logarithmic or a logistic function, with the aim of investigating whether this improves the correlation within and between species. The similarity between two individuals may indeed depend more on the ratio between animal sizes rather than size difference, suggesting, in this case, a log transformation of sizes. Second, the correlation with respect to

time and space for different fish length groups between species is included in the model with the aim of analysing not only *intraspecific* size correlations but also potential *interspecific* correlation between species according to size. This is accomplished for fish species that are potential competitors or predators upon each other (e.g., [12,13]) in the WBS such as cod and whiting.

The below hypotheses are accordingly tested:

> **H01**: For each species (cod and whiting), the correlation in fish density depends on space and fish size. The correlation is a structured, separable size-space correlation. The space correlation depends on the geographical distance and the size correlation on the distance in transformed size between fish. The transformation is a specified function parameterised on, e.g., the natural, logarithmic, logistic or other transformation scales.
>
> **H02**: For the two analysed species and for a given time period, there is a species correlation given the structured fish size and spatial correlations in fish density. Thus, there is a correlation in fish density between the two species.
>
> **H03**: For the two analysed species, there is a time correlation between two time periods for a given species, given the structured fish size and spatial correlations in fish density. Thus, there is correlation in fish density between years for each fish species.

The purpose of the present study is to provide an extension of the methodology to obtain more precise estimates of relative fish density patterns, which are a prerequisite for environmental impact assessments, including spatial explicit fisheries and fish resource management and advice as well as marine management and spatial planning from a cross-sector perspective [14]. For the Baltic, a better estimation of underlying relative resource density and availability for fishery will, among other things, enable more precise description of fisheries and individual vessel-based specific fishing power, fish catchability, and partial fishing mortality [15,16,17,18]. The methodology is extended here by not only using information on correlations in distribution patterns according to time and space between size groups within the different fish species [3] but also now considering the correlation in distribution of different sizes of groups between certain species that are expected to have interspecific interactions. The latter aspect can improve multi-species assessments and advice considerably by not only considering feeding analyses of fish in the multi-species models [19,20] but also integrating information on actual mutual distribution patterns and their correlations of the species predating on or competing with each other in the marine ecosystems.

Materials and Methods

1. Survey data used in the analyses

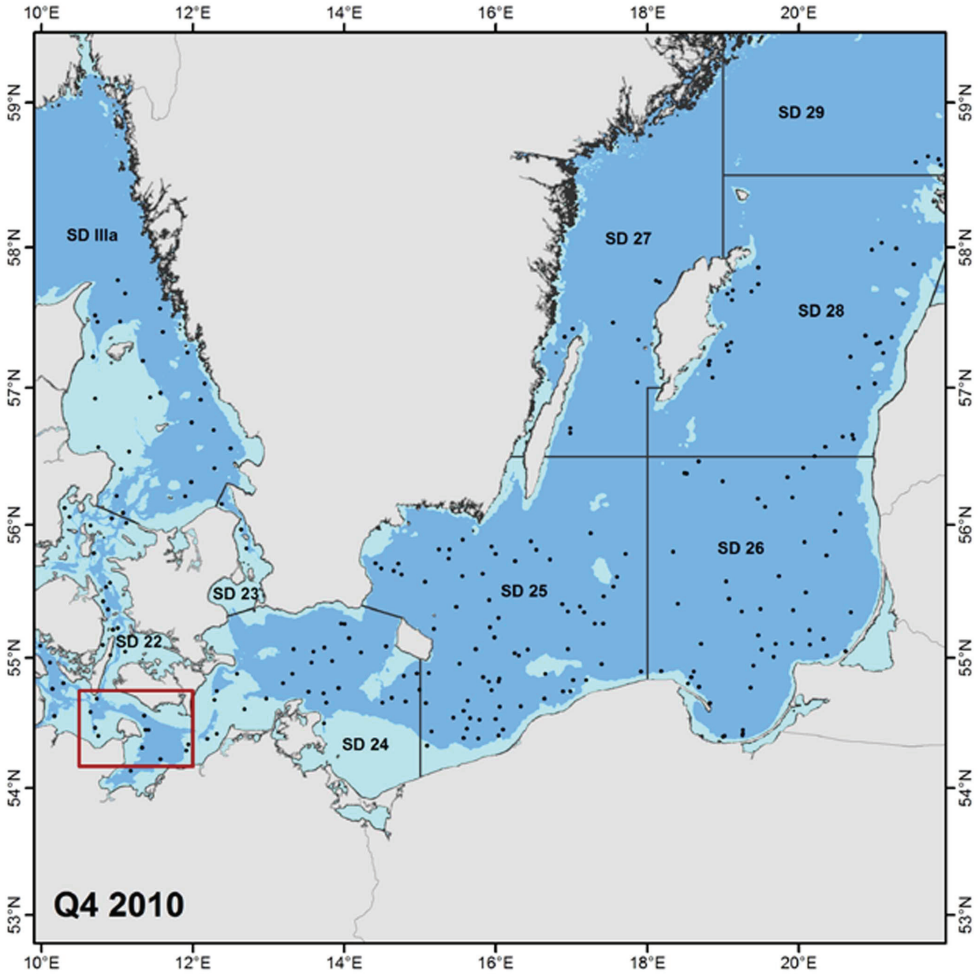
The international standardised ICES BITS survey is conducted in quarter 1 and quarter 4 of the year [21]. In 2001, the EU research project ISDBITS introduced a completely revised standard BITS survey [22,23,12,21] with the aim of introducing new demersal survey gear and a revised stratified random survey design, expanding seasonal and geographical sampling to obtain better coverage of especially cod distribution areas in all life stages and also for other species, including herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). In the traditional BITS, the participating nations used very different trawls, usually equipped with large bobbins, causing smaller cod to escape under the footrope [24]. ISDBITS employed new standardised survey trawls in addition to a standardised data sampling and processing design [22,21]. The new sampling design has broader geographical coverage in the 1st and 4th quarters of the year (Fig. 1) and is based on random selection of haul positions. The number of hauls is selected partly according to the respective fraction in area of different depth zones in the Baltic ICES subareas (60% of the hauls) and the 5-year running means of cod aggregations (catch rates) (40% of the hauls) estimated in previous surveys). Furthermore, statistically robust and standardised inter-calibration methods to link old and new survey data time series have been implemented [23,21]. Accordingly, the quality of the BITS survey data has, for the most recent 12-year time series, increased for demersal species, which allows obtaining of recruitment, density and abundance of age estimates at a higher coverage [12,21].

Extended local-scale BITS surveying was conducted in the Fehmarn Belt area of the WBS from 2009–2012 on a quarterly basis using the same survey design (Fig. 1) and the data was linked to the standard large scale ICES BITS survey data time series. Figure 1 shows examples of coverage for the standard and extended BITS surveys. The extension has included extra trawl hauls for quarters covered by standard surveying (quarters 1 and 4) as well as repetition of the extension hauls here for the quarters not covered during standard surveying (quarters 2 and 3). Accordingly, data with higher spatial and seasonal resolution has been obtained to inform the statistical survey analyses with the LGCP model.

Several round fish, flatfish, and clupeoid species were abundant in the catches of the combined surveys. Initial analyses indicated that the species and size correlations do not have a simple structure but are rather variable for most of the species combinations. This variation was expected as the species-specific habitats and biological inter-specific relations are likely to be different according to size. However, consistent density patterns over years and quarters were found according to size-specific abundance distributions for cod and whiting. The detailed distribution patterns of cod and whiting according to size group are described in Supporting Information Appendix A for the period 2009–2012, quarters 1 and 4. The present study concentrates on model runs with cod and whiting data from 2009 and 2010, quarter 4. The raw data analysed here consists of the number of fish caught by 1-cm size class per haul.

2. Statistical model used and its further development

The LGCP model provides, similar to other models in the family of correlation models [8,10], unbiased relative densities with a high resolution in time and space and by size/age for survey data by predicting and interpolating unobserved densities at any location in the covered area [1,2,3]. The formal model and its hierarchical structure are presented in Kristensen et al. [3] with a description how the model estimates latent, unobserved variables and how the goodness of fit (GOF) is determined (the latter is in the supplementary material). It is a counting model describing the discrete catch in number of observations, including zero observations. The model estimates spatial and temporal correlations between observations and includes zero observations, i.e., no-catch hauls, and over-dispersion parameters (Eq. 1) to enable analysis of all underlying survey data distributions. The LGCP model is a multivariate Poisson-lognormal distribution model, meaning that the catches in number observations are Poisson-distributed with mean densities following a multivariate lognormal distribution. The Poisson process is regarded as the sampling process generated by the fishing where there is an assumed spatial correlation between densities as a decreasing function of the geographical distance between them. The model parameters are obtained by maximum likelihood enabling interpolation and prediction of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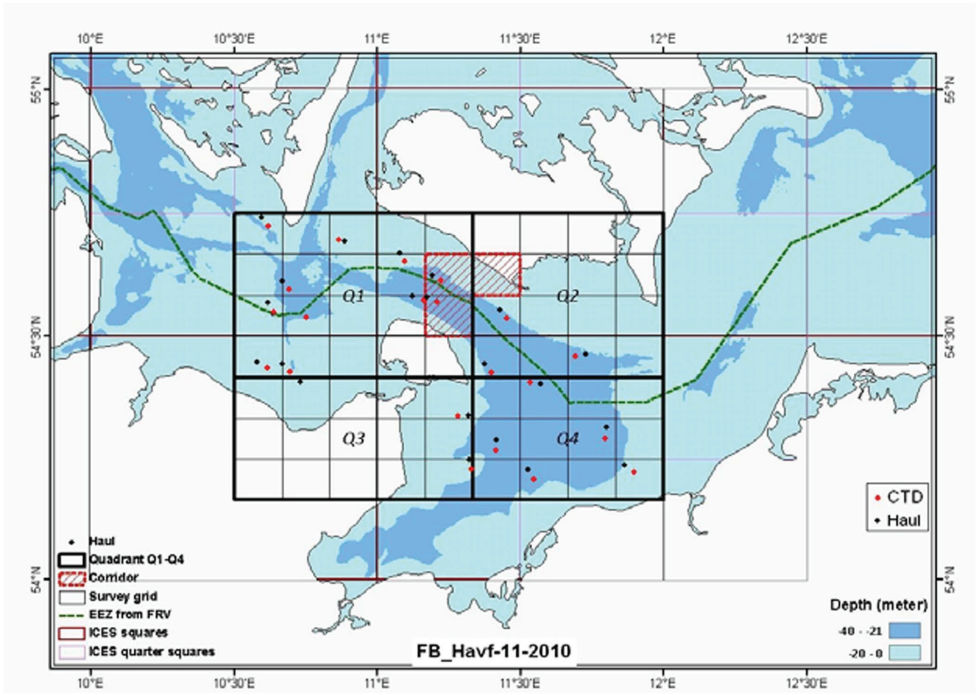
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CTD
Haul
Haul
Quadrant Q1-Q4
Corridor
Survey grid
EEZ from FRV
ICES squares
ICES quarter squares
Depth (meter)
-40 - -21
-20 - 0
FB_Havf-11-2010

Figure 1. Investigation area and coverage of the stratified random and standardized ICES BITS trawl survey with new survey design according to Nielsen *et al.* [22] and Lewy *et al.* [23]. The stratified random haul locations are black dots (upper panel) and the additional coverage for the extended BITS survey in the Fehmarn Belt Area of the Western Baltic Sea with haul locations are indicated by black dots and associated hydrographical CTD stations as light dots (lower panel), exemplified for the quarter 4 2010.
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unobserved densities at any point in space and time and enabling goodness-of-fit tests [2,3].

The models considered are characterised by explicit modelling correlation in space, size and species of survey density data. Single species, multispecies, and multiyear extension models are described.

3. The single species model, including size and space correlation

The correlation structure describes the spatial distribution of a single species of all size-classes *for a time-snapshot*. Here, a snapshot refers to approximately one month, i.e., the duration of the surveys analysed. The fish density modelling is based on considerations and testing of the processes acting on three different spatial scales (Hypothesis H01):

1. The large spatial scale size class variation is assumed to be an unstructured size distribution in the sense that the log-density of a size class s has a large scale mean of $\mu_i = \mu(s_i)$, $\mathrm{i} = 1, \ldots, \mathrm{k}$ where s_i denotes size class i and k is the number of size classes.
2. Spatial variations in log-density, $\eta(s,x)$, of a point in the space, x, for a given size are assumed random by nature, with some structure due to fish behaviour and ecology, as fish of similar sizes are expected to occupy the same spatial areas.
3. Small spatial scale variations, $\varepsilon(s,x)$, are assumed correlated across size-classes because of possible size-dependent schooling fish behaviour. Small scale variations can potentially be dominating in magnitude.

These three components suggest a model of the log density $\phi(s,x)$ of a size-class s in a spatial point x of the form

$$\phi(s_i,x_i) = \mu(s_i) + \eta(s_i,x_i) + \varepsilon(s_i,x_i) \qquad \text{(Eq.1)}$$

It should be noted that $\mu(s_i)$ includes the combined effect of large scale size distribution in the sea and the selection of the catch process (including gear selection, duration of haul and other global effects of the catch process). On the log scale, $\mu(s_i)$ is the sum of these two effects. In context of the present study, $\mu(s_i)$ should be considered as a nuisance parameter because here, we are only interested in the size-space correlation, $\phi(s,x)$, governing the log density as function of size and space. We make no assumptions on the structure and distribution of the combined large scale size distribution and gear selection, $\mu(s_i)$, which accordingly is unconstrained. As a part of the model validation, the consistency has been checked between estimates of $\mu(s_i)$ versus the spatial averaged count observations (CPUE, catch per unit of effort) across sizes, and the values were found to be consistent. The unconstrained model used here is in contrast to the approach in Kristensen et al. [3] where an *a priori* model for the $\mu(s_i)$ values is used based on the parameterised functions of gear selection and the decaying size spectrum. The present approach avoids such assumptions.

The process η is defined through a covariance function. First, assuming separability between size and space, the covariance between two distinct size-classes at two different positions is

$$cov(\eta(x_1,s_1),\eta(x_2,s_2)) = \sigma_1^2 \rho(x_1,x_2)\gamma(s_1,s_2) \qquad \text{(Eq.2)}$$

where σ_1^2 describes the magnitude of the process, and ρ describes the spatial and γ the size correlation.

In the same manner, the small-scale noise contribution ε is defined through its covariance function

$$cov(\varepsilon(x_1,s_1),\varepsilon(x_2,s_2)) = \sigma_2^2 1_{(x_1=x_2)}\gamma(s_1,s_2) \qquad \text{(Eq.3)}$$

stating that this contribution only acts locally in space ($1_{(x_1=x_2)}$) with the size correlation, $\gamma(s_1,s_2)$, and with a total magnitude determined by σ_2^2. The size correlation, γ, is assumed to be the same for the covariance of both η and ε. To understand the impact of Eq. 3, it is useful to view it in context of the stochastic processes in the following two scenarios. (1) For a fixed s, the $\varepsilon(x_1,s_1)$as function of x becomes white noise with intensity σ_2^2. This reflects the uncertainty of the catch process when repeating a haul at a nearby position (we never have observations at exactly the same position with total spatial overlap). (2) For a fixed x, the $\varepsilon(x_1,s_1)$as function of s is correlated according to $\gamma(s_1,s_2)$. This reflects the within-haul size correlation. For further detailed reasoning and field ground evidence of this effect (Eq. 3), we refer to Kristensen et al. [3].

Next, we turn to the question how to parameterise the spatial correlation between two points $\rho(x_1,x_2)$ and the size correlation between two size groups $\gamma(s_1,s_2)$. Most often, e.g., in kriging [25], the spatial correlation $\rho(x_1,x_2)$ is assumed to be a function of the Euclidean distance $|x_1 - x_2|$. This, however, does not account for the possible complex geographical structure and variability of the sea. Rather, it is desirable to compute the covariance accounting for all possible paths to get from x_1 to x_2 through the water area, with short paths weighing more than long paths. This feature is obtained by modelling ρ by using a Gaussian Markov random field [3,26]. This means that, instead of modelling the covariance, the precision matrix Q is the basis for the modelling (Q is the inverse covariance matrix):

$$Q_{ij} = \begin{cases} -1/\sigma^2 \text{ if } i \text{ and } j \text{ are neighbours} \\ (NC_i + \delta)/\sigma^2 \text{ if } i = j \\ 0 \quad \text{otherwise} \end{cases} \qquad \text{(Eq.4)}$$

where i and j are grid points; NC_i is the number of neighbours of the grid point i, on a lattice grid (cell size 20*20 km); δ and σ are positive parameters of the random fields. If point i is an inner point, $NC_i = 4$ while boundary points have fewer neighbours. In Eq. (4), the spatial correlation increases when δ decreases, and the correlation between two points depends on the geometry of the grid. The properties of the Gaussian Markov random field covariance (Q^{-1}) generated from Eq. 4, which gives a decreasing correlation according to distance, taking into account the geometry of the grid, is shown in Figure S1. Another example of this is shown in Kristensen et al. [3 in Fig. 2D].

Regarding the size correlation $\gamma(s_1,s_2)$, there are a number of options. The first option is the free unconstrained correlation

$\gamma(s_1,s_2)=\Sigma_{s_1,s_2}$ where the only requirement is that Σ must be a positive definite correlation matrix. This model is called the *unconstrained size correlation model.*

It is convenient to reduce this model to a simpler structure where the correlation between size classes only depends on the distance between the size classes. However, this assumption has been modified to account for more complex correlation structures. Instead of just applying a correlation function, where the correlation decreases when the distance increases, we further extend the autocorrelation function between sizes with a periodic factor in Eq. (5):

$$\gamma(s_1,s_2)=\gamma(\Delta s)=\exp\left(-\frac{\Delta s}{a}\right)\left(c+\cos\left(2\pi b\frac{\Delta s}{a}\right)\right)(1+c)^{-1} \quad \text{(Eq.5)}$$

where the distance in size (cm) is $\Delta s=|s_1-s_2|$. Note that this autocorrelation in one-dimension (size) is permissible (positive definite) according to Bochner's theorem [26]. The function contains the free parameters (a,b,c), where a is a scale parameter; b describes the periodicity; c describes the minimal amplitude of the oscillations. Thus, the correlations can become negative. In the case of $b=0$, an exponential decreasing correlation is obtained. When Δs increases, the oscillation amplitude decreases towards zero, and the correlation converges to zero. The Eq. (5) size correlation model is flexible and allows for a possible decrease in correlation between close fish sizes (small distance in size) up to a certain level and then increases again for very different fish sizes (large distance in size), which may occur when smaller and larger fish occupy the same areas.

Third, instead of the distance between actual fish sizes, we may alternatively let the correlation depend on the distance between transformed sizes. For example, the similarity between two individuals may depend more on the ratio between animal sizes rather than size difference, suggesting, in this case, a log transformation of sizes. In addition to considering the distance on the natural scale, we thus as well consider the log and the logistic transformations such that the distance in the log case is defined as $\Delta s=|log(s_1)-\log(s_2)|$. A logistic transformation is also investigated (Eq. 6) taking into account that the rate of change in distribution is small between the 1-cm groups for smaller and larger fish (high correlation), whereas for the medium-sized fish, the change in distribution is fast between 1-cm-groups (lower correlation).

$$logistic(s)=\frac{1}{1+\exp(-\alpha(s-l_{50}))} \quad \text{(Eq.6)}$$

The eq. (5) models, where Δs is based on the natural, the log scale and the logistic scales, are denoted models *parameterised on the natural, the log and on the logistic scale, respectively*. L50 is the size where we observe the highest rate of change in the spatial surface, and alpha measures that rate (the higher alpha is, the higher rate the rate is).

4. The multi-species extension of the model, including species correlation

The models from the previous section can be applied independently for two species A and B:

$$\begin{aligned}\phi_A(s,x)&=\mu_A(s)+\eta_A(s,x)+\varepsilon_A(s,x)\\ \phi_B(s,x)&=\mu_B(s)+\eta_B(s,x)+\varepsilon_B(s,x)\end{aligned} \quad \text{(Eq.7)}$$

where the correlation patterns of the stochastic processes η_A, ε_A, η_B and ε_B are estimated separately for each species.

In particular, the terms η_A and η_B are independent and therefore have a covariance matrix of the form

$$V\begin{pmatrix}\eta_A\\ \eta_B\end{pmatrix}=\begin{pmatrix}\Sigma_A & 0\\ 0 & \Sigma_B\end{pmatrix} \quad \text{(Eq.8)}$$

In a multi-species context, the dependence between η_A and η_B needs to be introduced. We describe and test two species correlation models: the *unconstrained species-size extension* and the *separable species-size extension.*

4.1 The unconstrained species-size extension. Let $\Sigma_A=\gamma_{\mathrm{A}}(s_1,s_2)=\Sigma_{\mathrm{A},s_1,s_2}$, and $\Sigma_B=\gamma_{\mathrm{B}}(s_1,s_2)=\Sigma_{\mathrm{B},s_1,s_2}$ denote the size-correlation matrices of species A and B, respectively. The unconstrained extension of the correlation for the combined set of species A and B is then

$$\Sigma_{A+B}=\begin{pmatrix}\Sigma_A & \Sigma_{\mathrm{AB}}\\ \Sigma_{\mathrm{BA}} & \Sigma_B\end{pmatrix} \quad \text{(Eq.9)}$$

where $\Sigma_{\mathrm{AB}}=\Sigma'_{\mathrm{BA}}$ of dimension n_An_B is free to choose with the only requirement that $\Sigma_{\mathrm{A+B}}$ is positive definite. The Supporting Information Appendix B (part 3) shows that this requirement is fulfilled if $\Sigma_{\mathrm{BA}}=\Sigma_{\mathrm{B}}^{1/2}(\mathrm{I_B}+\mathrm{RR}')^{-1/2}\,\mathrm{R}\,\Sigma_{\mathrm{A}}^{1/2}$, where R is any matrix of dimension n_An_B and where $\mathrm{I_B}$ is the identity matrix.

The following properties hold for this extension:

- In terms of appropriate parameterisations, it has the right marginals for species A and species B, as selected from a prior single-species analysis.
- It has species independence as a special case ($\Sigma_{\mathrm{AB}}=0$), so that the independence assumption can be formally tested. Note, however, that this is generally a rather weak test for independence given the high degrees of freedom. Thus, it is desirable to reduce the model first to achieve a higher power of the independence test.

The unconstrained species-size extension of the model assumes that the random field parameters, δ (Eq. 4), affecting the degree of spatial correlation for each of the species are identical, i.e., $\delta=\delta_A=\delta_B$. To conclude the construction of a space-size-species random field, the two terms $\eta_A(s,x)$ and $\eta_B(s,x)$ (Eq. 7) are tied together through the space-size-species covariance matrix

$$V\begin{pmatrix}\eta_A\\ \eta_B\end{pmatrix}=\begin{pmatrix}\Sigma_A & \Sigma_{\mathrm{AB}}\\ \Sigma_{\mathrm{BA}} & \Sigma_B\end{pmatrix}\otimes\Gamma_\delta=\begin{pmatrix}\Sigma_A\otimes\Gamma_\delta & \Sigma_{\mathrm{AB}}\otimes\Gamma_\delta\\ \Sigma_{\mathrm{BA}}\otimes\Gamma_\delta & \Sigma_B\otimes\Gamma_\delta\end{pmatrix} \quad \text{(Eq.10)}$$

where $\Gamma_\delta=\mathrm{Q}^{-1}$ is the inverse of the precision matrix Q of the Gaussian Markov Random Field and where $\otimes$ denotes the Kronecker product [26]. Eq. (10) states that *space* and the combination *(species, size)* are separable factors. The dimension of $V\begin{pmatrix}\eta_A\\ \eta_B\end{pmatrix}$, the quadratic covariance matrix, is $k*(n_A+n_b)$, where k is the number of spatial gridpoints considered. As an example, the model states that the covariance between, e.g., $\eta_A(s_1,x_1)$ and $\eta_B(s_2,x_2)$ should be found as the product of the spatial covariance $\rho(x_1,x_2)$ and the combined species-size correlation of the pair $((A,s_1),(B,s_2))$. Note that separable extension (Eq. 10) of permissible covariances (e.g., one in size and one in space, i.e., multi-dimensional) is always again

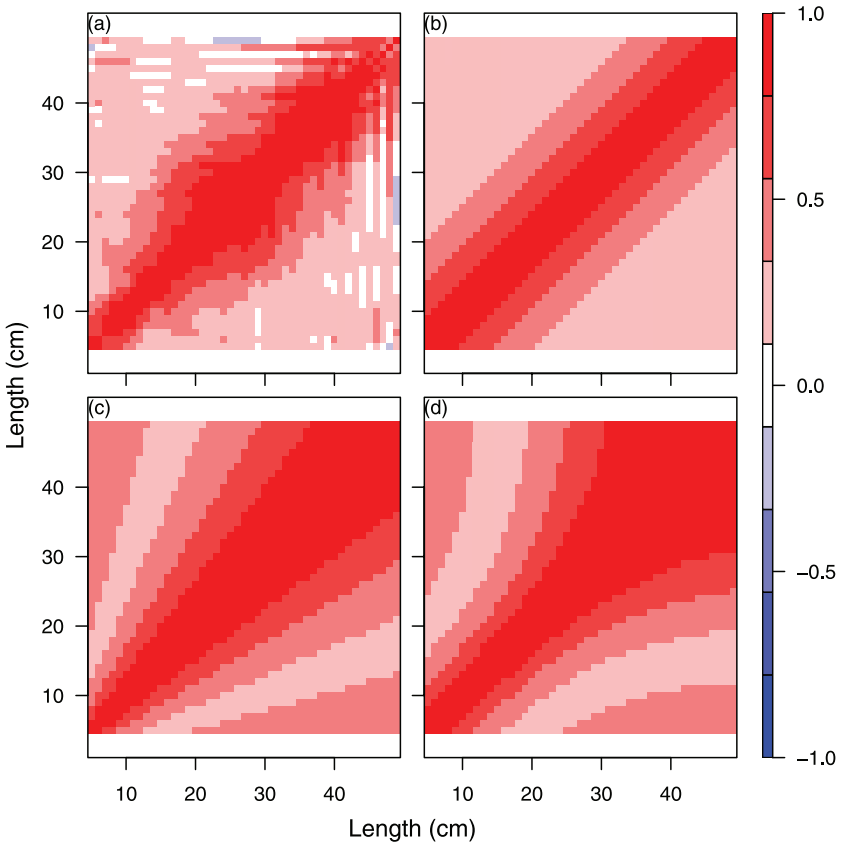

Figure 2. Comparison between fish size correlation matrix from different single-species model specifications for cod year 2009 quarter 4. SS1, Unconstrained free size correlation structure given as a positive definite correlation matrix (a); SS2, natural untransformed scale (b); SS3, log scaled (c); SS4, logistic scaled (d).
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permissible according to the rules following the Kronecker product [26].

The multispecies model based on Eq. (10) with species-specific size correlation as defined by Eq. (2) is denoted the *unconstrained species-size correlation with species-specific size correlation*. This means that the parameters in Eq. (5), a, b and c, depend on the species. A sub-model with a common size correlation (i.e., a, b, and c, not depending on species) and denoted *unconstrained species-size correlation with common size correlation* is considered as well.

4.2 The separable species-size extension. These models are based on and are sub-models of the unconstrained species-size correlation with common size correlation and attempt to measure the correlation, both within and between species, through the distance (dissimilarity) between transformed size groups.

More precisely, let t be a size-transformation function for the two species A and B. Consider two size groups s_1^A and s_2^B for the two species, and define the covariance between them as

$$\Sigma_{A+B}(s_1^A, s_2^B) = \gamma(t(s_1^A), t(s_2^B))\tau(A,B) \qquad \text{(Eq.11)}$$

where γ (Eq. 2) is a common correlation function valid for both species on the transformed size scale, and $\tau(A,B)$ denotes the overall species correlation between A and B, i.e.,

$$\tau(u,v) = \begin{cases} 1 \; if \; u = v \\ \rho \; if \; u \neq v \end{cases} \qquad \text{(Eq.12)}$$

where u and v are in $\{u,v\} \in \{A,B\}$. This MS3 model based on Eqs. (10), (11) and (12) is denoted the *separable* model and $MS3 \subset MS2 \subset MS1$; See Table 1.

As Σ_{A+B} is a parameterised sub-model of the unconstrained correlation Σ_{AB} in Eq. (10), the separable model is a sub-model of unconstrained species-size correlation with common size correlation. The model states that to measure the correlation between two species A and B of sizes s_1 and s_2, we should first transform their sizes to a common scale at which a generic covariance function γ applies and finally multiply by the overall species correlation. The natural and the log scale are applied as size scaling functions. We chose the log model instead of the logistic model because they perform equally well, but the log model has fewer parameters and thus is more convenient to apply. Finally, we contrasted the model MS3, including interspecific spatial correlations, with a sub-model, MS4, for which there is no assumed species correlation (i.e., $\rho = 0$) *denoted independence*.

Although multispecies models combine species, spatial and size correlations separately for each year, the exact same type of models are considered, where species and year switch roles. These models are called multi-year models, where for each species, the correlation between year, space and size is modelled.

4.3 Model overview. An overview of the models considered and tested is given in Table 1, where single, multispecies and multiyear models are covered. In addition, the hierarchical structure of the model testing is indicated.

Table 1. Overview of the models considered and tested, where single, multispecies and multiyear models are covered. In addition, the hierarchical structure of the model testing is indicated.

Type of Model	Model		Parameters
Single Species - including size and spatial correlation	SS1	Unconstrained	Σ, δ, σ_1^2, σ_2^2
	SS2	Structured parameterised on natural scale	a, b, c, δ, σ_1^2, σ_2^2
	SS3	Structured parameterised on log scale	a, b, c, δ, σ_1^2, σ_2^2
	SS4	Structured parameterised on logistic scale	α, l_{50}, a, b, c, δ, σ_1^2, σ_2^2
Multi-Species - including species, spatial and size correlation	MS1	Unconstrained species-size correlation with species specific size correlation	a_x, b_x, c_x, δ, σ_{x1}^2, σ_{x2}^2, x = species A B, $R_{n_A \times n_B}$
	MS2	Unconstrained species-size correlation with common size correlation	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, $R_{n_A \times n_B}$
	MS3	Separable model	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, ρ
	MS4	Independence	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, $\rho=0$
Multi-Year - including yearly, spatial and size correlation	MY1	Unconstrained year-size correlation with species specific size correlation	a_x, b_x, c_x, δ, σ_{x1}^2, σ_{x2}^2, x = year A B, $R_{n_A \times n_B}$
	MY2	Unconstrained year-size correlation with common size correlation	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, $R_{n_A \times n_B}$
	MY3	Separable model	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, ρ
	MY4	Independence	a, b, c, δ, σ_{x1}^2, σ_{x2}^2, x = A B, $\rho=0$

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The hierarchical order of the models is as follows:

$$SS2 \subset SS1 \text{ and } SS3 \subset SS1$$

$$MS4 \subset MS3 \subset MS2 \subset MS1$$

$$MY4 \subset MY3 \subset MY2 \subset MY1$$

This states that the $SS2$ and $SS3$ models are sub-models of the $SS1$ model.

Finally, we illustrate the potential of an extended correlation structure by predicting the abundance distribution of a target species, using only indirect data, i.e., data of the other species at the same year *or* the same species the year before. For the cases of cod and whiting in 2009 and 2010, the possible correlation across species and year are further investigated. We illustrate the potential of the correlation model to make spatial abundance predictions, first using species correlation models and secondly using time correlation models.

5. Ethics Statement

No humans, primates or laboratory animals were involved in the study. There was no sampling from private land, and the field studies did not involve endangered or protected species. Only fish sampled in public sea areas have been used. All fish were sampled with research survey trawls under or related to ICES (International Council for Exploration of the Sea; www.ices.dk) coordinated international standard trawl surveying. The sampling and handling of fish strictly followed all ICES guidelines, procedures, legislative rules, and permissions from national governments for sampling and handling of fish in fisheries research surveys. The sampling was conducted by national government-owned research vessels following Danish national legislation, permissions, and ethics for handling of wild caught fish. The sampling was performed under repeated international standardised surveying where the research vessels had full permission to sample from all relevant national public authorities (governments) in the Baltic waters.

There was no approval of this study by an Institutional Animal Care and Use Committee (IACUCO) or Ethics Committee. This was not necessary because the sampling and handling of fish strictly followed all ICES guidelines, procedures, legislative rules, and permissions from national governments for sampling and handling of fish in fisheries research surveys. The sampling was conducted by national government-owned research vessels following Danish national legislation, permissions, and ethics for handling of wild-caught fish.

Results

1. Single-species models

The results of the four separate single species analyses, SS2-SS5, of cod and whiting in the fourth quarter in 2009 and 2010 are shown in Figures 2, 3, S2, and S3 and Table 2 and Table S1 in File S1. The different size correlation structures tested are shown separately in the 4 panels of each figure, covering an hierarchical testing procedure (see Fig. 2 text). The detailed distribution patterns of cod and whiting according to size group are described

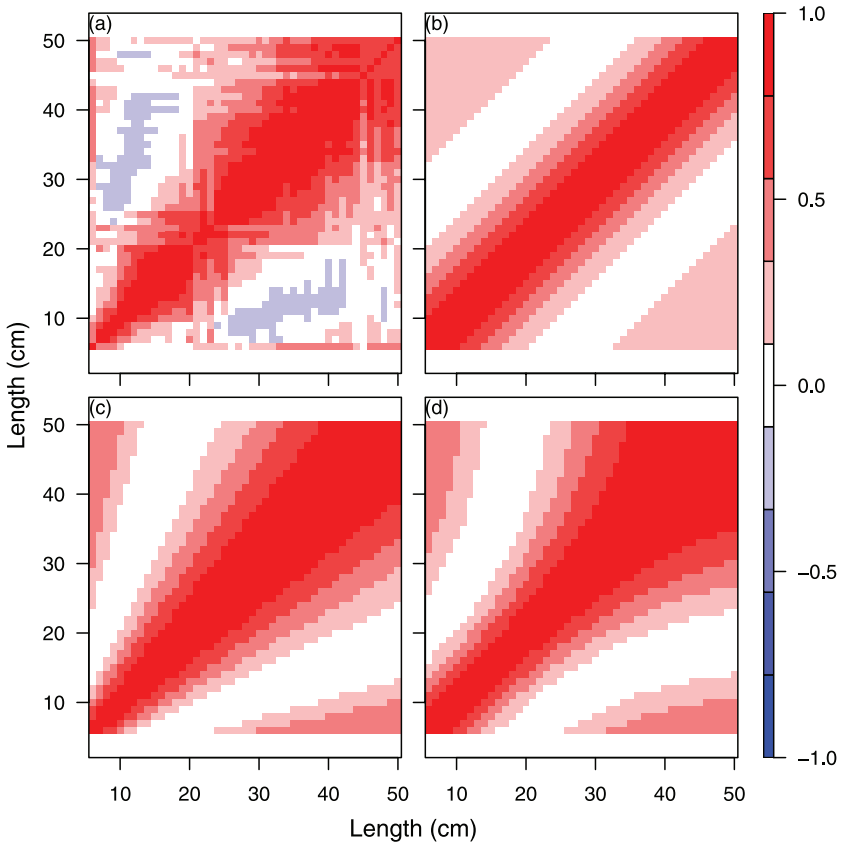

Figure 3. Model comparison for cod year 2010 quarter 4. SS1, unconstrained (a); SS2, natural scale (b); SS3, log scaled (c); SS4, logistic scaled (d).
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in Supporting Information Appendix A for the period 2009–2012, quarters 1 and 4.

The main purpose of the tests was to investigate for each species and year which of the size correlations models that could be rejected or not (Hypothesis H01 and the models SS2, SS3 or SS4). It was especially important to establish whether the free unconstrained model could be reduced to a structured model so that abundance predictions could be made using a model with few parameters. All models were parameterised from the same correlation function (Eq. 5) on the transformed scale. The spatial correlation parameter was first tested for independence of size and time for each species and both years, and it was found that it was possible to distinguish between the space and size-time correlation. The Chi-Square likelihood ratio tests of the different models SS1. SS2, SS3, and SS4 (Table 2 and Table S1 in File S1) did not have sufficient power to reject any of the correlation structures for both cod and whiting in 2009 and 2010 because of the very high number of degrees of freedom in the main model. This indicates that there is no significant difference between (SS1) and (SS2, SS3, and SS4) with respect to the description of the correlation between size groups for cod any of the years (Table 2), and consequently we cannot reject a structured correlation model (hypothesis H01).

Higher power of the tests can be obtained by re-binning the data to 2-cm size groups and re-fitting the models (SS1)–(SS4), as this will very much reduce the degrees of freedom of model (SS1). When using 2-cm size groups, the test results for cod in both 2009 and 2010 (not shown) came out in favour of the log- and logistic transformations parameterising a structured size correlation model, as the identity transform was rejected ($p<0.02$). Thus, the identity transformation was excluded from the analysis. There is a trade-off between precision in the model by using 2-cm size groups compared with the high resolution in the rate of change in distribution when using 1-cm groups. In the present approach, we use the 1-cm groups to retain as much information as possible in the distribution dynamics of the fish. On average, a juvenile Baltic cod grows 1 cm in 6 weeks, and when using 2-cm size groups, the time resolution of 1.5 months is considered too high.

Consequently, a size-structured model cannot be rejected for any of the species for both years. In the multi-species and -year model extensions, the log transformation parameterisation was chosen because it is simpler than the logistic transformation in the sense that it does not contain any further parameters.

An alternative criterion for model selection is parameter consistency over time. In this case, the question regarding the four independent analysis (Figs. 2, 3, S2, S3) is which one of the transformation functions for the structured size correlation models (SS2)-(SS3) will have the most robust parameter estimates. In other words, are the images Figure 2c and Figure 3c (or 2d or 3d) for cod significantly different? Likewise, is this the case for Figure S2c and Figure S3c (or S2d and S3d) for whiting? Parameter estimates related to the logistic (d) and log (c) transforms display equal consistency over time, and here we have reported the results of the log-transform (c) (Table 3). All correlation parameters (a,b,c) (Eq. 1) related to size can be tested independent of the year effect, and, furthermore, the spatial correlation parameter δ appears independent of both year and species (Table 3). It is remarkable that the

Table 2. Model comparisons with unconstrained size correlation versus natural, log and logistic scaled and model reductions according to either species or year.

Model or Structure of correlation	Tot Df	Deviance	Chisq	Df	Pr(>Chisq)
Model comparison, cod year 2009 quarter 4					
(SS1) Unconstrained	993	−122858.25			
(SS2) Natural	6	−122607.85	250.40	987	1.000
(SS3) Log	6	−122700.71	157.54	987	1.000
(SS4) Logistic	8	−122693.00	165.25	985	1.000
Model comparison, cod year 2010 quarter 4					
(SS1) Unconstrained	993	−133760.09			
(SS2) Natural	6	−133241.87	518.22	987	1.000
(SS3) Log	6	−133336.41	423.68	987	1.000
(SS4) Logistic	8	−133325.86	434.23	985	1.000
Model reduction: cod+whiting year 2009 quarter 4 by structure of species correlation					
(MS1) Unconstrained species correlation	1451	−226997.63			
(MS2) Common correlation function	1449	−226984.52	13.11	2	<0.010
(MS3) Separable	10	−226433.58	550.94	1439	1.000
(MS4) Independence	9	−226430.51	3.08	1	0.079
Model reduction: cod year 2009+2010 quarter 4 by structure of year correlation					
(MY1) Unconstrained year correlation	2036	−256427.46			
(MY2) Common correlation function	2034	−256423.99	3.47	2	0.176
(MY3) Separable	10	−256055.89	368.10	2024	1.000
(MY4) Independence	9	−256028.29	27.59	1	0.000

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parameter *b*describing the angular velocity of the oscillating part (Eq. 5) of the size-correlation is significantly different for cod and whiting, explaining the main differences in the species specific size correlation functions (Fig. 4). This result basically indicates that small and large cod occur in the same spatial regions, whereas this is not the case for whiting. This pattern is also visible from the initial analyses with animations of cod and whiting abundance patterns across size-groups from the surveys as described in Supporting Information Appendix A, i.e., where the whiting is observed more westerly as smaller individuals and more easterly as larger fish, whereas small cod are observed more easterly both for the very small and very large size classes. Consequently, there is a rather consistent structure in the size correlation within the species over time.

2. Multispecies models including species correlation

The next step is to use the model to assess the possible correlation between species to test hypothesis H02. This is accomplished by comparing the four multispecies correlation models MS1–MS4 and testing whether the free, unconstrained species-size model MS1 can be reduced to the sub-models M2–MS4.

The combined analyses with the multi-species extension of the model considering species correlation involved runs under the log-transformed size for both species (Figs. 5, 2009 and S4, 2010). The results are presented in Figure 5 for 2009 and Figure S4 for 2010 and are covered in detail in the panel (a) that presents an image of the combined correlation of cod (the large square block) and whiting (the smaller square block) using the previous (separate) analysis for each species combined with the assumption of unconstrained species-size correlation between the two species. The next panel (b) is visually very similar to panel (a) and represents the model reduction where cod and whiting are assumed to have a common correlation function. Despite the visual similarity between panel (a) and (b), the likelihood ratio test strongly rejects this reduction (Table 2). Panel (c) is an image of the

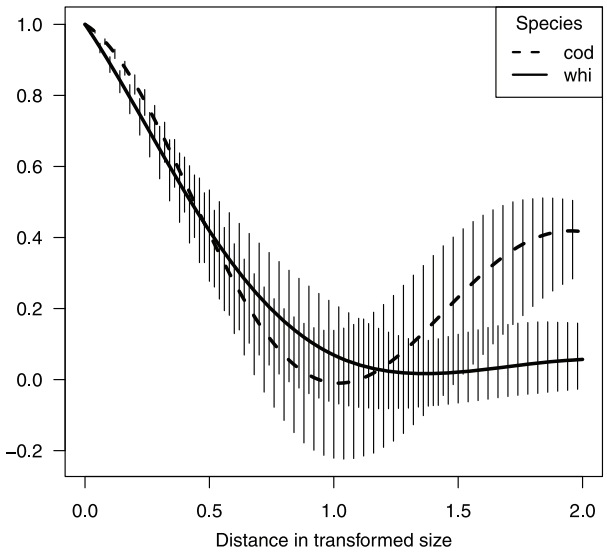

Figure 4. Estimated correlation (y-axis) for different size correlation functions, Eq. (5), of cod and whiting (single species runs) using the log transform model parameters given by Table 3. The vertical bars indicate the 95% confidence intervals.
doi:10.1371/journal.pone.0099151.g004

Table 3. Summary of single species runs: Parameter estimates of log-transform model and size-correlation (first 5 parameters) plus spatial covariance parameters (final 9).

	Estimate	Std. Error
a_{cod}	2.42	0.26
a_{whi}	0.98	0.11
b_{cod}	1.19	0.16
b_{whi}	0.35	0.09
c	0.98	0.26
$\log\delta$	−7.02	0.57
$\log\sigma_1^{cod\ 2009}$	0.61	0.06
$\log\sigma_1^{cod\ 2010}$	0.37	0.08
$\log\sigma_1^{whi\ 2009}$	0.53	0.08
$\log\sigma_1^{whi\ 2010}$	0.24	0.12
$\log\sigma_2^{cod\ 2009}$	−0.47	0.14
$\log\sigma_2^{cod\ 2010}$	−0.05	0.11
$\log\sigma_2^{whi\ 2009}$	0.31	0.09
$\log\sigma_2^{whi\ 2010}$	0.29	0.09

Valid parameter reduction applied over time and for some species parameters.
doi:10.1371/journal.pone.0099151.t003

separable model reduction, and this model does not fit very well. Finally, panel (d) shows the model fit, assuming species independence. The likelihood ratio tests for (c) and (d) indicate that it is not possible to distinguish between (b), (c) and (d). In summary, none of the model reductions are valid because of the rejection of model (b) because of the combined nested structure of the test procedure. Consequently, (a) will have to be chosen as final model in this case, i.e., no constraints in the species correlation. The conclu are the same for cod and whiting in 2010 (Fig. S4), except that here the separable model visually appears to perform better than for 2009, and the species correlation is significantly non-zero. Below, we return to the overall conclusions on species correlation.

3. Multiyear analyses including year correlation

In MY1–MY4, the cod-whiting species correlation has been replaced by the corresponding 2009–2010 year correlation to test hypothesis H03. For both species (cod 2009 and 2010 in Fig. 6, and whiting 2009 and 2010 in Fig. S5), the common correlation function hypothesis in (b) cannot be rejected as $p \approx 0.18$ and $p \approx 0.05$, for cod and whiting, respectively (Table 2 and Table S1 in File S1). Furthermore, the separable model (c) cannot be rejected, but the independence test (d) is rejected for both species. Consequently, for both species, one will select model (c), i.e., a separable correlation model, as the final model.

4. Summary of the results

Three main conclusions can be drawn. i) For the single species models, the size correlation models parameterised on natural (SS2), log (SS3) and logistic scale (SS4) cannot be rejected compared with the unconstrained model (SS1). ii) The unconstrained species and year correlation models MS and MY 1–3 are all generalizations of the single species models SS 1–4. iii) Both multispecies and multiyear correlations (unconstrained) appear to occur (see Figures 5, 6, S4, S5 panels (a) and (b)). For the multiyear correlation models, it was possible to obtain a parameterised year correlation model, the separable model MY3, which was not rejected, and this indicates that Hypothesis H03 can be accepted. In contrast, we cannot reject that species correlation occurs (hypothesis H02), but this correlation is very complex and resisted the parameterisation described here. The current models appear to perform better when describing time correlation than species correlation. A free, unconstrained species-size correlation model with many parameters is therefore still needed for describing the correlation between species.

5. Predicting abundance surfaces

The potential of the correlation model to make abundance surface predictions was analysed, first using (unconstrained) species correlation models (Figs. 7 and S6) and second using time correlation models (Figs. 8 and S7). An extended species or time correlation structure is useful to predict abundance surfaces of a target species when using only indirect data, i.e., data of the other species at the same year *or* the same species the year before. For all figures, the left panels represent the "observed" patterns (single species model predictions), and the right panels represent the corresponding predicted panels. The visual inspection reveals that of the performance of all predictions, the species-based predictions are perhaps the most accurate. These findings also support that we cannot reject hypothesis H02 when using a much more complex model in this comparison, i.e., the unconstrained species correlation model with many parameters, to perform the species-based predictions.

Discussion

1. Trawl survey analysis model development and general application

A length-based stochastic model of single-species stock dynamics including densities [6] was applied to the Baltic cod species based exclusively on survey data; however, this model was not spatially explicit. In the present study, an extension of the statistical LGCP model [3] is applied to the standard and extended BITS data for Baltic cod and whiting to investigate not only intraspecific size correlations, including spatial and temporal distribution patterns, but also potential interspecific correlation between species in relative density according to space, size, and time.

The motivation for developing size-based density models including species, time and spatial correlation is based on the apparent visual relationship between species from sequential abundance maps (as for instance presented in Figures 7, 8, S6, S7, first column, illustrating the spatial distribution by species by size group as well as described in Supporting Information Appendix A). Quantification and modelling of the covariance functions is performed either for the same species at different time periods or for different species at the same time. The aim is to empower spatial predictions of relative density of fish within and across species after constructing spatial abundance models that support hypotheses testing regarding alternative model specifications. Such species/size time/size correlation models are high dimensional, and model reduction is sought to apply the models for predictions. We formulated natural model reduction hypotheses based on a size transformation that results in fish being able to be compared on a size scale.

2. Structure of size correlation models by species and size transformations used for model parameterisation

The separate single species analyses assumed that the spatial and the size correlations in density are independent among species. The analyses further revealed that the idea that fish can be compared on a size scale by transformations of the natural size

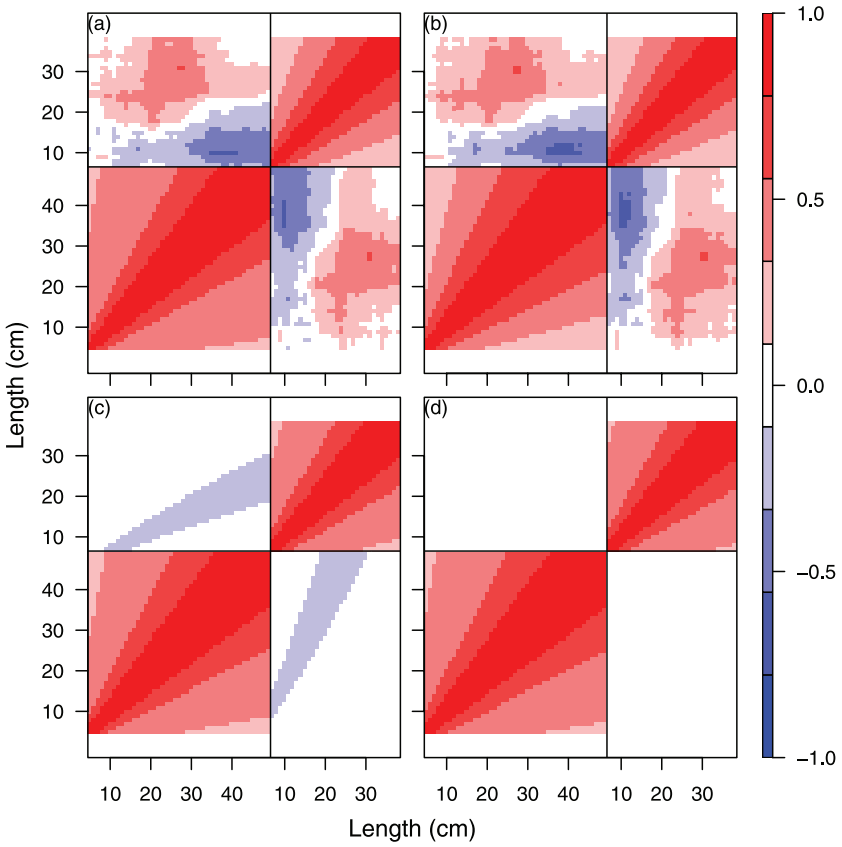

Figure 5. Multispecies models for cod and whiting year 2009 quarter 4. MS1, unconstrained species correlation with separate parametric size correlation for each species (a); MS2, unconstrained species correlation with common parametric size correlation for both species (b); MS3, separable species-size correlation (c); MS4, no species correlation (d).
doi:10.1371/journal.pone.0099151.g005

scale cannot be rejected for any of the species for both years, and there is a rather consistent structure in the size correlation within species over time. The log and logistic size transformations, but not the natural (no transformation) for cod, were not rejected when changing the bins to 2-cm length groups. On this basis, hypothesis H01 cannot be rejected. As such, the model enables prediction, interpolation and animation of unobserved relative distribution and density patterns at any location and season of the year in the area for, e.g., cod and whiting.

3. Multi-species and multi-year correlation models according to model complexity

Regarding model complexity, the following conclusions have been drawn. For the relation between a year and the subsequent year of the spatial distribution of a given species/size, the simple reduced low dimensional model is adequate to describe the complicated observed correlation patterns, and a significant correlation between years was found. For the multispecies relationship, the simple structured models developed are not adequate to describe the correlation pattern, and thus, we were not able to decide if a significant species correlation exists. This indicates that the separable model is found too simple to describe the potential species/size correlation. However, it is remarkable how well the (unconstrained) species correlations model can predict a "missing" species, which indicates that species correlation may exist, and we cannot reject hypothesis H02. In general, the strength in the approach lies in the detailed description and testing of the combination of species-size and time-size correlations.

For the single species models, area and time spatial variations in log fish density, $\eta(s,x)$, of a point in the space, x, for a given size are assumed random by nature. However, if some structure in relative fish densities according to animal behaviour exists, we expect to observe fish of similar sizes occupying the same spatial areas. For the two competing species, cod and whiting, we expect that fish of similar sizes of occupy the same spatial areas (sharing the same habitats, food sources, etc.) or fish of different sizes occupy the same spatial areas (due to predation on each other and even potential cannibalism). Both cod and whiting have, for the North Sea, been demonstrated to be competing species for the same habitats and to predate on each other (e.g., [13]). Interspecific relationships may play a role in the distribution patterns of WBC cod and whiting, but this phenomenon is not well understood [27,28,29,19]. There is spatial and temporal variation in biological interactions due to predation by cod in the Baltic Sea, where also cannibalism has been documented as an impacting factor in certain periods [30,31,20,12,32]. The levels of cannibalism are dependent on the abundance of juveniles and larger cod predators, their overlap in distribution, and the availability of alternative prey items for larger cod, such as sprat and herring [33,34,20,32]. In the WBS, there are also abundant competing gadoid predators in the form of whiting [12].

The basic single species model used (Eq. 1) includes three processes: large spatial scale variations for each size group, small-

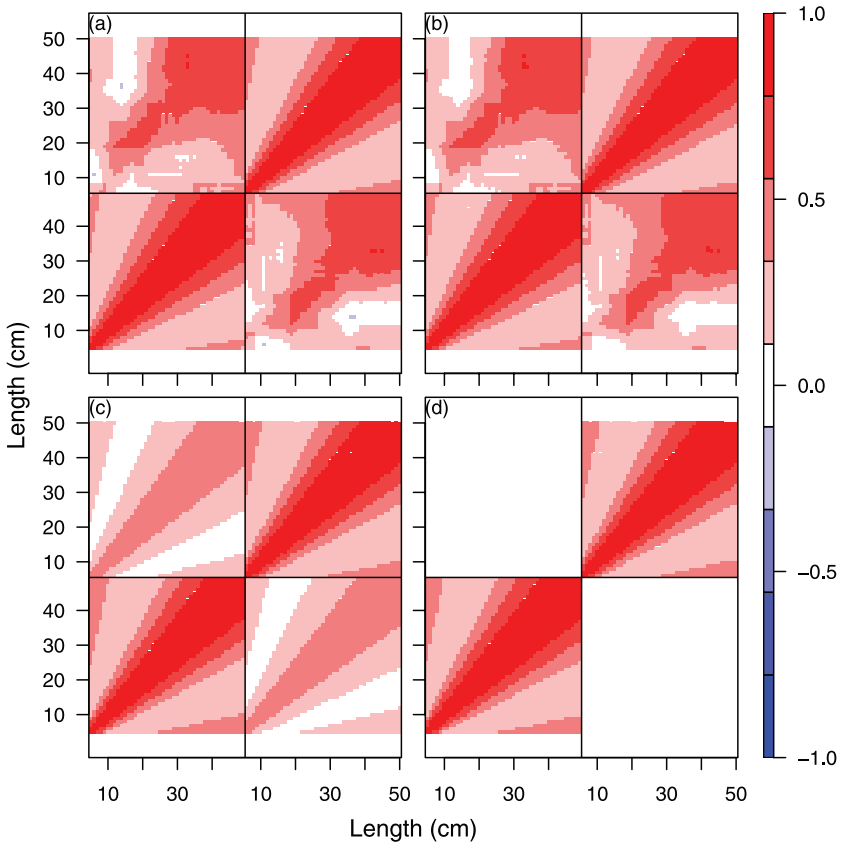

Figure 6. Multiyear models for cod year 2009 and 2010 quarter 4. Unconstrained year correlation with separate parametric size correlation for each year (MY1, a), Unconstrained year correlation with common parametric size correlation for both years (MY2, b), separable year-size correlation (MY3, c), No year correlation (independence) (MY4, c).
doi:10.1371/journal.pone.0099151.g006

scale variations and a spatial/size correlation component describing the spatial landscape by size. The large-scale variation is chosen as generally as possible, i.e., an unconstrained model including a parameter for each size group. The small-scale variation and correlation are assumed to be the same for each point in the space and depends only on the size correlation. The spatial/size correlation was modelled using a Gaussian random field, for which all possible ways between two spatial points are evaluated and for which shorter paths are preferred to longer paths. This model has the advantage that paths crossing land can be avoided.

For the multispecies models including species correlation, it was assumed that the parameters affecting the degree of spatial correlation are assumed to be the same for the species considered. This may be incorrect for species with different spatial behaviour. Similarly, for the multiyear analyses, it was assumed that these parameters are the same for the time periods considered.

Whether all of these assumptions are too restrictive or not depends on the species and time periods considered and must be tested statistically in each case. The results indicate all single species models and assumptions for cod and whiting in the WBS are not rejected. The same applies to the multiyear analyses, whereas the multispecies structured models are rejected.

It should be noted that estimation of spatially aggregated absolute abundance demands correction for bias in the log-normal distribution, especially if data are far from Gaussian. However, for constant variance fields, the correction has no effect on relative abundance as used here. Estimation of absolute abundance is usually performed by posterior simulation as demonstrated by, e.g., Lewy and Kristensen [2]. The present paper does not include this problem because we consider all mean value parameters, $\mu(s_i)$, as nuisance parameters where we operate with relative abundance surfaces rather than simulating and predicting absolute abundance.

4. Further extension of the correlation structures and future studies

In the present analyses, we assume that there is no difference in the small- and large-scale size correlations [3]. In addition, we assume that the small-scale variations, $\varepsilon(s,x)$, i.e., the within haul variations, are correlated across size-classes because of possible size-dependent schooling [3]. As small-scale variations can potentially be dominating, future studies should analyse differences in the large scale and small scale variation in relation to species, and an improved model should take into account differences between large-scale and small-scale variation.

For the multi-species extension, a structured size correlation model is used where correlations between size classes only depend on the distance between transformed sizes and where a common parameterisation on the different size transformation scales are applied (involving log transformed size) for both species. The same function for distance between transformed sizes does not

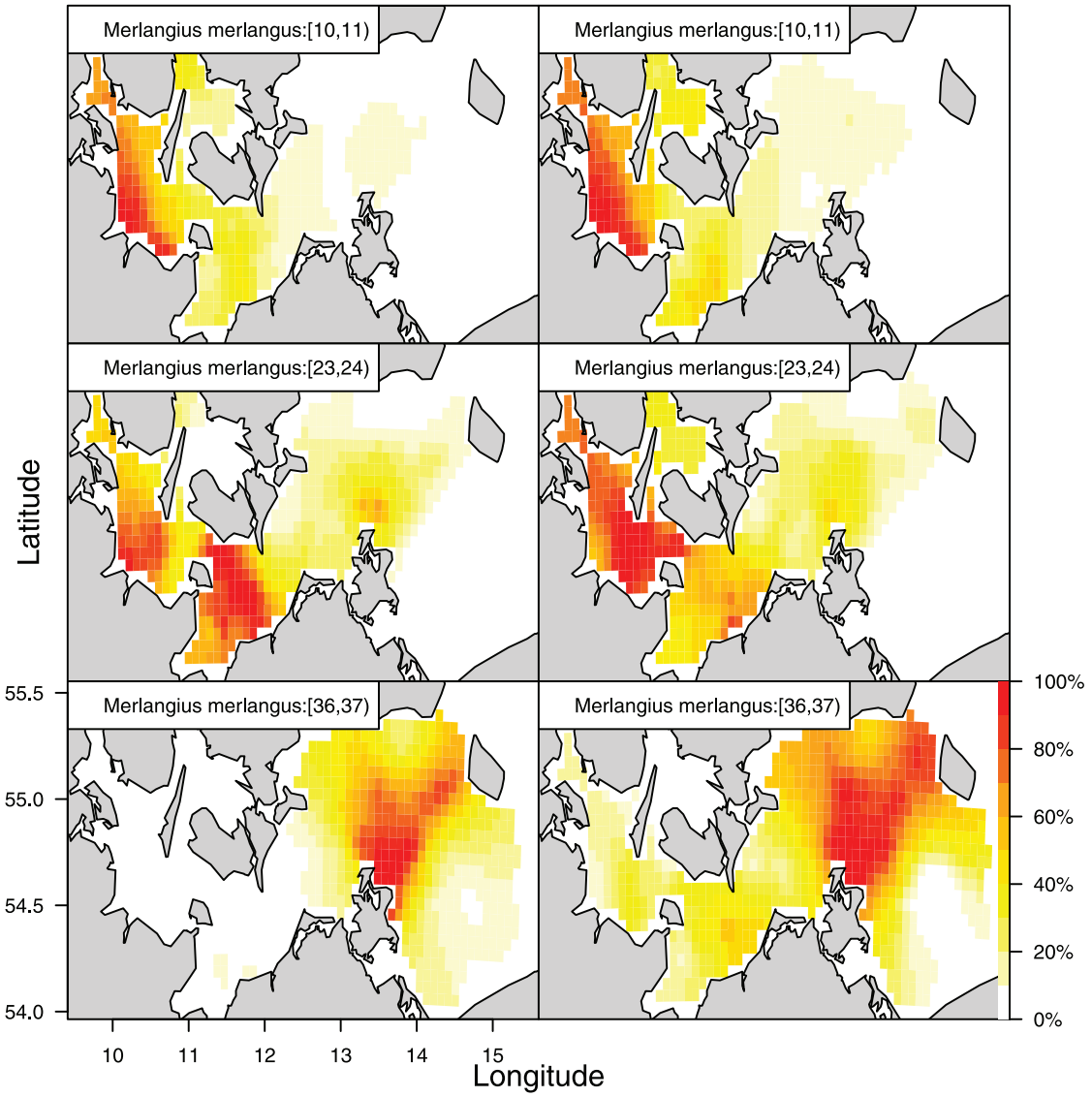

Figure 7. Maps of relative whiting abundance 2009/Q4 *based on whiting observations* (left column) versus the same maps *based on cod observations* (right column) utilizing MS1 model of Table 2. The three row panels indicate three whiting size groups in cm.
doi:10.1371/journal.pone.0099151.g007

necessarily need to be used for both species. Figure 4 indicates that the parameter b, which describes the angular velocity of the oscillating part of the size-correlation, is significantly different for cod and whiting, explaining the main differences in the species specific size correlation functions when applying the same size correlation structure (i.e., the same size class transformation). Higher correlation between species might have been achieved by applying different functions according to distance in transformed size where more complex species specific structures are taken into account. Future studies should investigate further alternative species specific functions for transformation of size to parameterise the same size correlation model.

The present analyses have only covered model development and data analysis of observations from relatively few years, quarters and species. Further studies should investigate the structure of the correlation models and their size transformation parameterisations as well as the multi-species correlation models for an extended set of years, quarters and fish species.

The purpose of our study was to establish a correlation structure describing the spatial distribution and relative density patterns of a single species of all size-classes *for a time-snapshot* (1 month). Our modelling of animal density is based on considerations and testing of the processes acting on a spatial scale using survey catch rates by size group by haul. Alternatively, future studies could consider combining the existing area-based time snapshot models with new models tracking the movements in time. Perhaps such models modelling the correlation between the directional movements could better capture the fish behaviour and the resulting spatial fish distribution.

Finally, model-based geostatistical methods can be further applied to investigate optimal survey designs for different species

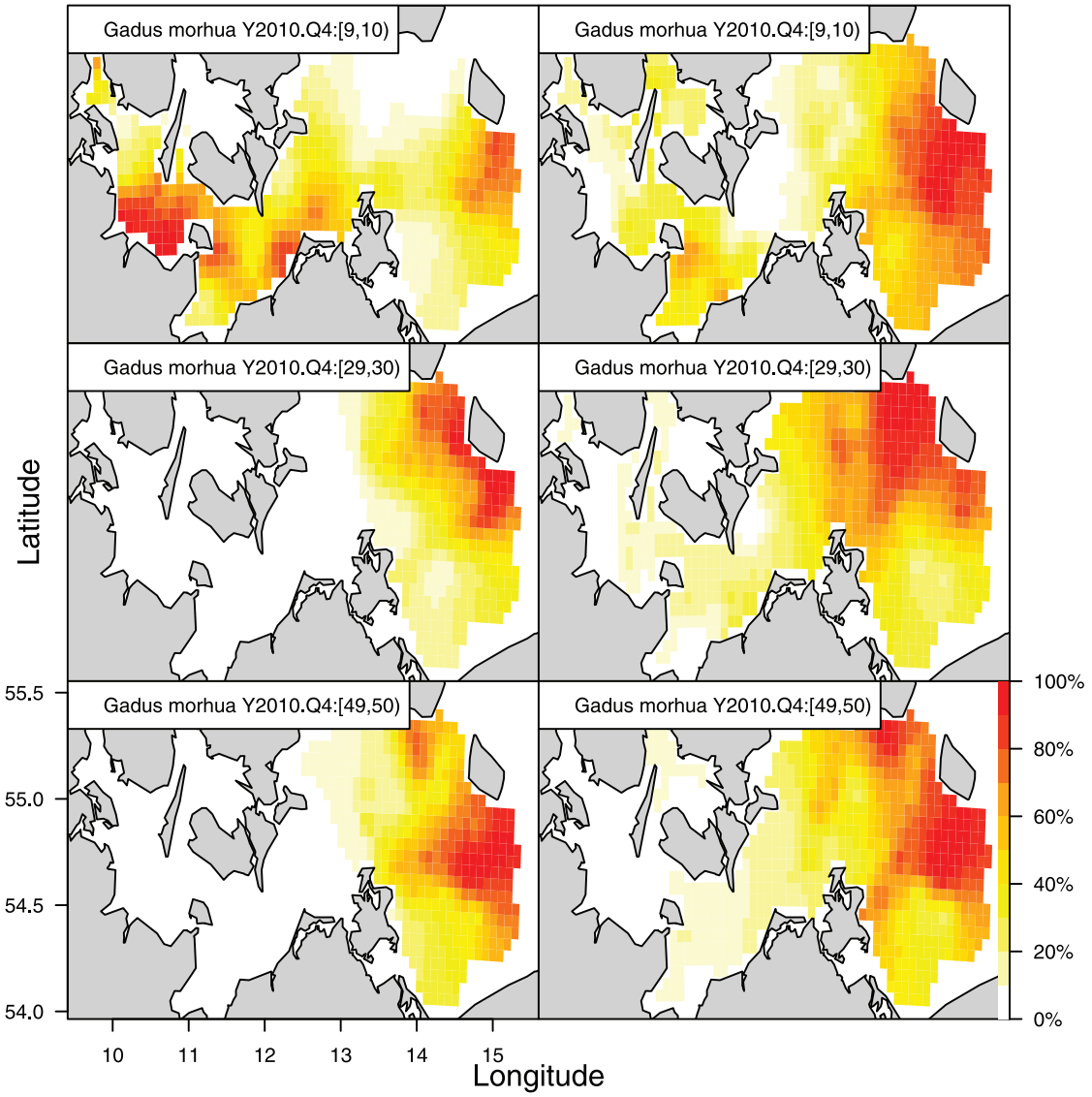

Figure 8. Predictive power of the models illustrated by maps of relative cod abundance 2010/Quarter 4 based on *cod observations that year* (left column) versus the same maps based on *cod observations previous year* (right column) utilizing model MY3. The three row panels indicate three cod size groups in cm.
doi:10.1371/journal.pone.0099151.g008

and size groups using the extended BITS survey dataset established here.

Supporting Information

Figure S1 Spatial correlation measured from given centre point. It shows the properties of the Gaussian Markov Random field co-variance (Q^{-1}) generated from Eq. 4, which indicates a decreasing correlation according to distance taking into to account the geometry of the grid. The co-variance (correlation) depends on all possible ways between two points, i.e., it is an integral over all possible ways between the centre point and any other point weighted with the distance of the way (in the sea and not over land).
(TIF)

Figure S2 Model comparison for whiting year 2009 quarter 4. SS1, unconstrained (a); SS2, natural scale (c); SS3, log scale (d); SS4, logistic scaled (d).
(EPS)

Figure S3 Model comparison for whiting year 2010 quarter 4. SS1, unconstrained (a); SS2, natural scale (b); SS3, log scaled (c); SS4, logistic scaled (d).
(EPS)

Figure S4 Multispecies models for cod and whiting year 2010, quarter 4. See figure explanation for Figure 5.
(EPS)

Figure S5 Multiyear models for whiting year 2009 and 2010 quarter 4. See figure explanation for Figure 6.
(EPS)

Figure S6 Maps of relative whiting abundance 2010/Q4 *based on whiting observations* (left column) versus the same maps *based on cod observations* (right column) utilizing MS1 model of Table S1 in File S1. The three row panels indicate three whiting size groups in cm.
(EPS)

Figure S7 Predictive power of the models illustrated by maps of relative whiting abundance 2010/Quarter 4 based on *whiting observations that year* (left column) versus the same maps based on *whiting observations previous year* (right column) utilizing model MY3. The three row panels indicate three whiting size groups in cm.
(EPS)

File S1 Table S1, (containing model comparisons with unconstrained size correlation versus natural, log and logistic scaled, and model reductions according to either species or year for whiting year 2009 quarter 4, whiting quarter 4 2010, cod+whiting year 2010 quarter 4, and whiting year 2009+2010). Keywords; Appendix A (with description of specific distribution patterns for cod and whiting for different size groups); Appendix B (with description of methods on (B1) how to parameterise a general positive definite (PD) correlation matrix ϕ? R?, (B2) how to parameterise a general positive definite correlation matrix with given marginal, and (B3) the proof for this).
(DOC)

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Author Contributions

Conceived and designed the experiments: JRN. Performed the experiments: JRN. Analyzed the data: JRN KKR PL FBA. Contributed reagents/materials/analysis tools: JRN KKR PL FBA. Wrote the paper: JRN KKR PL. Revising the manuscript critically for important intellectual content: JRN KKR PL FBA. Interpretation of the data: JRN KKR PL FBA. Final approval of the version to be published: JRN KKR.

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Survey gear calibration independent of spatial fish distribution

Peter Lewy, J. Rasmus Nielsen, and Holger Hovgård

Abstract: Trawl surveys provide important information for evaluation of relative stock abundance fluctuations over time. Therefore, when survey gears or vessels are changed, it is important to compare the efficiency and selectivity of old and new gears and vessels. A method for estimation of conversion factors is developed based on a survey design where paired hauls are taken in the same trawl track line. The method explicitly accounts for changes in fish density caused by trawling disturbance. A generalized linear model for paired hauls catches is analytically derived and the gear conversion and disturbance parameters with their precision are obtained using standard software. Simulation studies carried out additionally showed that the estimated conversion factors were practically unbiased. Because of the independence of the spatial fish distribution, the new method is preferable to the traditional paired hauls design for which it is generally not possible to obtain the statistical properties of the estimated conversion factors. The paper is concluded with suggestions on how to optimize survey design. The method was used to estimate conversion factors for Atlantic cod (*Gadus morhua*) from Danish gear calibration experiments in the Baltic Sea.

Résumé : Les inventaires au chalut fournissent des données importantes pour l'évaluation des fluctuations temporelles de l'abondance relative des stocks. Lorsqu'on change les engins de pêche ou les navires qui servent à l'inventaire, il est important de comparer l'efficacité et la sélectivité des anciens et des nouveaux engins ou navires. Nous avons mis au point une méthode pour estimer les facteurs de conversion nécessaires, basée sur un plan d'inventaire dans lequel des traits de chalut appariés sont réalisés sur une même ligne de pêche. La méthode tient compte de façon explicite des changements de densité des poissons qui résultent des perturbations causées par le chalutage. Nous avons obtenu analytiquement un modèle linéaire généralisé des récoltes appariées et nous avons estimé les paramètres de conversion des engins et les paramètres de perturbation, de même que leur précision, à l'aide de logiciels communs. De plus, des études de simulation montrent que les facteurs de conversion estimés sont pratiquement sans erreur. À cause de l'indépendance de la répartition spatiale des poissons, la nouvelle méthode est préférable aux plans habituels de récoltes appariées dans lesquels il n'est généralement pas possible d'obtenir les propriétés statistiques des facteurs de conversion estimés. Nous concluons par des suggestions pour optimiser le plan d'inventaire. Nous avons utilisé la méthode pour estimer les facteurs de conversion pour des données sur la morue franche (*Gadus morhua*) provenant d'expériences danoises de caractérisation d'engins de pêche faites dans la Baltique.

[Traduit par la Rédaction]

Introduction

Time series of catch rates in trawl surveys are important sources of information for tracking the development in fish stock abundance and are often used to calibrate analytical stock assessments. Sometimes it is necessary to introduce new survey vessels or to change the fishing gear (e.g., ICES 1992; Nielsen et al. 2001), which destroys the continuity of the survey time series data. In these cases, it is necessary to compare the efficiency and the selectivity of the old and new gears (or vessels) and to estimate conversion factors that allow the catches taken in the historical period to be expressed in units compatible with the new standard.

When reviewing the literature, Pelletier (1998) noted that the experimental designs used for calibrating trawl survey gears may broadly be classified into two groups: (*i*) paired hauls methods where stations close in time and space are selected on the tacit assumption that fish density is the same (e.g., Sissenwine and Bowman 1978; Wilderbuer et al. 1998) or (*ii*) area-based methods where the fish density and size structure are assumed to be homogeneous within particular strata (e.g., Ehrich 1991). Despite the difference in survey design, the estimation of conversion factors is often based on classical statistical methods, i.e., lognormally distributed catches combined with linear models accounting for gear and location and haul effects (Robson 1966; Sissenwine and Bowman 1978; Wilderbuer et al. 1998). Other estimates are based on the relationship between catch per unit effort (CPUE) of two gears (Wilderbuer et al. 1998). Kappenman (1992) developed an estimator based on the assumption that

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the distribution of paired CPUEs of the two gears considered are identical except for the scale parameters. Warren (1997) applied a log-linear model based on the CPUE ratio. For a paired trawl design where two vessels are trawling at the same time with a distance ranging from 0.25 to 1 nautical mile, Pelletier (1998) applied a quasi-likelihood method assuming that the mean values of the abundance associated with the paired hauls are identical.

In the present paper, we consider the special case of the paired hauls design where the successive hauls are taken in the same track line within a short time range. This design has previously been used for trawl comparison (Wilderbuer et al. 1998; ICES 2002) and for comparing different coastal gears (Methven and Schneider 1998). This design is preferred because it reduces the spatial variability of fish density to a minimum and thus justifies the assumption that the fish density is the same for each of the two paired hauls. However, fishing in immediate succession in the same track creates a new problem, as the first haul may affect the fish density available for the second haul by removing fish or by inducing changes in behaviour that alters fish distribution. This effect, which is termed the disturbance effect, therefore needs to be estimated and accounted for.

The purpose of the present work is to develop a method for gear calibrations that is independent of the fish density, which is treated as nuisance parameter, and includes estimates of the conversion factor and the disturbance effect of both the new and the old gear. The method is expressed as a generalized linear model (McCullagh and Nelder 1989) that allows the precision of the parameters to be estimated and hypotheses to be tested using standard software. The method is used to analyse Danish calibration experiments carried out as part of the Baltic International Trawl Survey (Nielsen et al. 2001; ICES 2002).

Methods

Formulation of the statistical model

The statistical model is based on a survey design where two hauls are taken successively in the same track line where it is acknowledged that the first haul affects the fish density available to the second haul. The disturbance caused by the first haul is assumed to be dependent on the gear actually used but being independent of fish density and habitat. The disturbance effect is the net effect of removing the fish caught and affecting the fish behaviour, which includes both attraction of fish to and repulsion of fish from the track line. Theoretically, the disturbance effect can be both positive and negative dependent on whether fish are mainly attracted or repulsed.

When comparing two gears, a total of four possible types of experiments can be carried out. They are classified as follows: type 0, the experiment for which the old gear is applied twice; type 1, a haul of the old gear is followed by a haul of the new gear; type 2, a haul of the new gear is followed by a haul of the old gear; type 3, the new gear is applied twice.

Let $U^{\text{seq}}_{\text{type},l,s}$ denote the CPUE for a given experiment type, temporal sequence of the hauls seq, length group l, and station s, where seq = 1, 2 and type = 0, 1, 2, 3. It is assumed that all CPUEs are Poisson distributed with mean equal to gear catchability multiplied by the fish density. For the second haul, fish density is assumed to be affected by the disturbance effect. Finally, it is assumed that the CPUEs for the first and second haul given the fish density are independent variables. The model is summarized in eqs. 1–4:

	First haul	Second haul
(1) Type 0	$E(U^1_{0,l,s}) = q_{\text{old},l}D_{0,l,s}$	$E(U^2_{0,l,s}) = q_{\text{old},l}\alpha_l D_{0,l,s}$
(2) Type 1	$E(U^1_{1,l,s}) = q_{\text{old},l}D_{1,l,s}$	$E(U^2_{1,l,s}) = q_{\text{new},l}\alpha_l D_{1,l,s}$
(3) Type 2	$E(U^1_{2,l,s}) = q_{\text{new},l}D_{2,l,s}$	$E(U^2_{2,l,s}) = q_{\text{old},l}\beta_l D_{2,l,s}$
(4) Type 3	$E(U^1_{3,l,s}) = q_{\text{new},l}D_{3,l,s}$	$E(U^2_{3,l,s}) = q_{\text{new},l}\beta_l D_{3,l,s}$

where E denotes the expected value, $q_{\text{old},l}$ and $q_{\text{new},l}$ are the catchabilities of the two gears, and D is the fish density at station s prior to the first haul. For the second haul, fish density is assumed to be affected by the disturbance caused by the first haul where α_l designates the disturbance effect of the old gear and β_l the disturbance effect of the new gear. The parameters α_l and β_l may be less or greater than 1, as no assumption is made on the net effect. As the catchabilities as well as the disturbance effects may differ by length, the equations are supplied with and index l reflecting different length classes.

The objective of the survey gear calibration is to estimate the conversion factors, that is, the ratios between the catchabilities, $\gamma_l = q_{\text{new},l}/q_{\text{old},l}$. It is immediately observed that the conversion factor cannot be estimated without estimating at least one of the disturbance parameters α_l and β_l.

Now let $U_{\text{type},l,s} = U^1_{\text{type},l,s} + U^2_{\text{type},l,s}$ denote the sum of CPUEs by type, length group, and station. As the CPUEs for given fish densities are assumed to be independent Poisson distributed variables, it is well known that the conditional distributions of $U^2_{0,l,s}|\,U_{0,l,s}$, $U^2_{1,l,s}|U_{1,l,s}$, $U^1_{2,l,s}|\,U_{2,l,s}$, and $U^1_{3,l,s}\,|U_{3,l,s}$ are binomially distributed $B(U_{\text{type},l,s}, p_{\text{type},l})$ for each type, length group, and station and where

$$(5)\quad p_{0,l} = \frac{E(U^2_{0,l,s})}{E(U^1_{0,l,s}) + E(U^2_{0,l,s})} = \frac{q_{\text{old},l}\alpha_l D_{0,l,s}}{q_{\text{old},l}D_{0,l,s} + q_{\text{old},l}\alpha_l D_{0,l,s}} = \frac{1}{1+1/\alpha_l}$$

$$(6)\quad P_{1,l} = \frac{E(U^2_{1,l,s})}{E(U^1_{1,l,s}) + E(U^2_{1,l,s})} = \frac{\gamma_l}{\gamma_l + 1/\alpha_l}$$

$$(7)\quad P_{2,l} = \frac{E(U^1_{2,l,s})}{E(U^1_{2,l,s}) + E(U^2_{2,l,s})} = \frac{\gamma_l}{\gamma_l + \beta_l}$$

$$(8)\quad P_{3,l} = \frac{E(U^1_{3,l,s})}{E(U^1_{3,l,s}) + E(U^2_{3,l,s})} = \frac{1}{1+\beta_l}$$

Equations 5–8 show that estimation of the absolute values of the catchabilities is not necessary (or possible).

The logits, $r_{\text{type},l}$, of the four probabilities are

$$r_{0,l} = \text{logit}(p_{0,l}) = \ln\left(\frac{p_{0,l}}{1-p_{0,l}}\right) = \ln(\alpha_l) = \theta_l$$

$$r_{1,l} = \text{logit}(p_{1,l}) = \ln(\gamma_l) + \ln(\alpha_l) = \pi_l + \theta_l$$

$$r_{2,l} = \text{logit}(p_{2,l}) = \ln(\gamma_l) - \ln(\beta_l) = \pi_l - \tau_l$$

$$r_{3,l} = \text{logit}(p_{3,l}) = -\ln(\beta_l) = -\tau_l$$

where

$$\pi_l = \ln(\gamma_l) = \ln\left(\frac{q_{\text{new},l}}{q_{\text{old},l}}\right), \theta_l = \ln(\alpha_l), \text{ and } \tau_l = \ln(\beta_l).$$

The four logits, $r_{\text{type},l}$, type = 0–3, can be combined into one linear equation:

$$(9) \quad r_{\text{type},l} = \pi_l x_{\text{type}} + \theta_l y_{\text{type}} + \tau_l z_{\text{type}}$$

where

$$x_{\text{type}} = \begin{cases} 0 & \text{if type} = 0 \\ 1 & \text{if type} = 1 \\ 1 & \text{if type} = 2 \\ 0 & \text{if type} = 3 \end{cases}$$

$$y_{\text{type}} = \begin{cases} 1 & \text{if type} = 0 \\ 1 & \text{if type} = 1 \\ 0 & \text{if type} = 2 \\ 0 & \text{if type} = 3 \end{cases}$$

$$z_{\text{type}} = \begin{cases} 0 & \text{if type} = 0 \\ 0 & \text{if type} = 1 \\ -1 & \text{if type} = 2 \\ -1 & \text{if type} = 3 \end{cases}$$

As the conditional distributions derived are binomial distributions and the logits (the canonical link function) are linear functions of the parameters, π_l, θ_l, and τ_l, the theory of generalized linear models (McCullagh and Nelder 1989) was applied to analyse the paired CPUE data. The model may be regarded as multiple linear regression with heterogeneous slopes and with x, y, and z as known covariates.

If the assumption of binomial distributed variables does not hold, an overdispersion parameter is estimated (McCullagh and Nelder 1989). Testing whether the conversions factors γ_l and the disturbance effects α_l and β_l differ across length classes is facilitated by the standard reformulation of eq. 9 to

$$r_{t,l} = \pi x_t + \pi_l x_t + \theta y_t + \theta_l y_t + \tau z_t + \tau_l z_t$$

and by testing the hypotheses $\pi_l = \theta_l = \tau_l = 0$.

The GENMOD SAS procedure (SAS Institute Inc. 1996) was used to estimate parameters and testing hypotheses. The Pscale option and Wald's statistics were used as a test to include overdispersion. Type3 contrast instead of Type1 analysis (SAS notation) was carried out because this is recommended in connection with Wald's statistics. This means that only the result of the first hypothesis tested can be used. When testing a new hypothesis, a new run must be carried out with a new model specifying the factors in the correct order.

Simulation study

Two main types of studies were carried out with the following purposes. The first was to investigate the bias of the estimated conversion factors using the new method based on the survey design where paired hauls are taken in the same trawl track line and, further, to compare the properties of the estimator derived with an alternative estimator. In this study, it was assumed for each station that the catches were based on fixed fish densities implying that only the catches generated varied in the simulations. All simulations were carried out for each length group separately and were based on the observed CPUEs and estimated values of both conversion factors and disturbance effects to reflect the conditions observed in the field experiments.

The second was to compare the new method with a paired hauls design, where the distance between nearby hauls is chosen to be as small as possible but without any kind of disturbance. The performance of the traditional paired hauls design heavily depends on the assumptions on spatial fish distribution. For the simulations comparing the two methods, a spatial distribution pattern has been chosen that is favourable for the traditional paired hauls design. The basic assumption is that the two fish densities at each of the paired nearby stations were drawn from the same statistical distribution. It was further assumed that the variance was the same for all stations. The variance measures the spatial inhomogeneity of the resource. One would expect that the paired hauls method is superior to the new method when the variance is small and vice versa. Both simulation procedures are described in Appendix B.

Optimal survey design

The field experiments included experiments of types 1–3 and enabled estimation of the conversion factor and the disturbance factor associated with both gears. However, as shown in Appendix A, if the full model eq. 9 is used, the estimator of the conversion factor only depends on data from experiments of types 2 and 3. The conversion factor could alternatively be estimated using experiments of types 0 and 1. The researcher should thus attempt to evaluate which of these two designs will lead to the most precise conversion factor estimate for a given research effort.

As shown in Appendix A, the conversion factor for a given length group applying data of types 2 and 3, $\hat{\gamma}_{2+3}$ is estimated by

$$\hat{\gamma}_{2+3} = \hat{\beta}\frac{1-\hat{p}_2}{\hat{p}_2}$$

where

$$\hat{\beta} = \frac{1-\hat{p}_3}{\hat{p}_3}$$

where $\hat{p}_2$ and $\hat{p}_3$ are defined by eq. A4 in Appendix A.

The variance of the estimated conversion factor can be approximated by

Table 1. Ground gear rigging and Scanmar trawl size measurements from the Danish calibration experiments in the Baltic Sea.

		Gear dimensions	
Gear	Ground gear rigging	Trawl height (m)	Door spread (m)
TV3	Rubber snake with inserted 15-cm rubber discs	6.0–8.0	60–85
Granton	Iron bobbins, diameter 40 cm	3.0–4.5	60–75

$$(10)\quad V(\hat{\gamma}_{2+3}) \approx \beta^2 \mathrm{VAR}\left(\frac{1-\hat{p}_2}{\hat{p}_2}\right) + \left(\frac{1-\hat{p}_2}{\hat{p}_2}\right)^2 \mathrm{VAR}(\hat{\beta}) = \left(\frac{\beta}{\gamma}\right)^3 \left(\frac{(\gamma+\beta)^2}{n_2} + \frac{(1+\beta)^2\gamma}{n_3}\right)$$

where n_2 and n_3 are the total number fish caught for both gears at all stations for type 2 and type 3 experiments, respectively. If n_{2+3} (= $n_2 + n_3$) is total number fish caught in the type 2 + type 3 experiments, the optimal distribution on the two types is (Raj 1968)

$$\frac{n_2^{\text{optimal}}}{n_{2+3}} = \frac{\gamma+\beta}{\gamma+\beta+(1+\beta)\sqrt{\gamma}}$$

$$\frac{n_3^{\text{optimal}}}{n_{2+3}} = 1 - \frac{n_2^{\text{optimal}}}{n_{2+3}}$$

Instead of a formulation based on number of fish caught, we prefer an equation that is based on number of hauls. The total mean number of fish caught at types 2 and 3 are proportional to $\gamma + \beta$ and $\gamma(1 + \beta)$, respectively. Using these values as relative weights, the optimal allocation of the number of hauls by the two types, m_2^{optimal} and m_3^{optimal}, becomes

$$(11)\quad \frac{m_2^{\text{optimal}}}{m_{2+3}} = \frac{\sqrt{\gamma}}{1+\sqrt{\gamma}}, \quad \frac{m_3^{\text{optimal}}}{m_{2+3}} = \frac{1}{1+\sqrt{\gamma}}, \text{ and}$$

$$m_{2+3} = m_2^{\text{optimal}} + m_3^{\text{optimal}}$$

The optimal solution only depends on the conversion factor and not on the disturbance. If $\gamma > 1$, i.e., the new gear is more efficient than the old gear, a larger proportion should be taken of the type 2 experiments and vice versa. For $\gamma = 1$, the optimal split is 0.5 for each of the type of experiments.

The minimum variance for type 2 + type 3 experiments, which corresponds to the optimal solution, is found by insertion of n_1^{optimal} and n_2^{optimal} into eq. 10:

$$V^{\min} \approx (\hat{\gamma}_{2+3}) \approx \frac{1}{n_{2+3}} \frac{\gamma}{\beta} (\beta + \gamma + (1+\beta)\sqrt{\gamma})^2$$

Similarly applying type 0 + type 1 experiments, the optimal minimum variance is

$$V^{\min}(\hat{\gamma}_{0+1}) \approx \frac{1}{n_{0+1}} \gamma\alpha \left(\frac{1}{\alpha} + \gamma + \left(1+\frac{1}{\alpha}\right)\sqrt{\gamma}\right)^2$$

The latter two equations are based on total the number of fish caught in both types 2 + 3 and 0 + 1, n_{2+3} and n_{0+1}, respectively. Again, we prefer to compare variances that are based on the number of hauls, as the total mean numbers of fish caught are proportional to $2 + \alpha(1 + \gamma)$ and $2\gamma + \beta(1 + \gamma)$ for types 0 + 1 and 2 + 3, respectively. The minimum variances can be approximated by

$$(12)\quad V^{\min}(\hat{\gamma}_{2+3}) = \frac{1}{m_{2+3}} \frac{1}{(2\gamma + \beta(1+\gamma))} \frac{\gamma}{\beta} (\beta + \gamma + (1+\beta)\sqrt{\gamma})^2$$

$$(13)\quad V^{\min}(\hat{\gamma}_{0+1}) = \frac{1}{m_{0+1}} \frac{1}{(2+\alpha(1+\gamma))} \times \gamma\alpha \left(\frac{1}{\alpha} + \gamma + \left(1+\frac{1}{\alpha}\right)\sqrt{\gamma}\right)^2$$

where m_{2+3} and m_{0+1} designate the total number of hauls.

Comparative fishing trials comparing survey gears

The survey gear calibration data were collected within a European Union Study Project (Nielsen et al. 2001). The objective of this project was to standardize the national abundance surveys in the Baltic Sea by introducing a common survey gear and to develop an internationally coordinated survey design. Here, the analysis is restricted to the Danish fishing experiments.

The Danish research vessel R/V *Dana* carried out the comparative fishing operations during the standard Baltic Atlantic cod (*Gadus morhua*) surveys in the first and fourth quarters during the period 1999–2002. The calibration stations were selected based on catch rates information available from the ongoing survey in an attempt to avoid comparisons in areas with low cod density. The gears compared were the Granton trawl traditionally used on the Danish surveys (ICES 1997) and the TV3 trawl, which is the new international standard (Nielsen et al. 2001; ICES 2002). The two gears differ by design and size and are equipped with different ground gears (Table 1). The fishery was only performed during daytime (light hours).

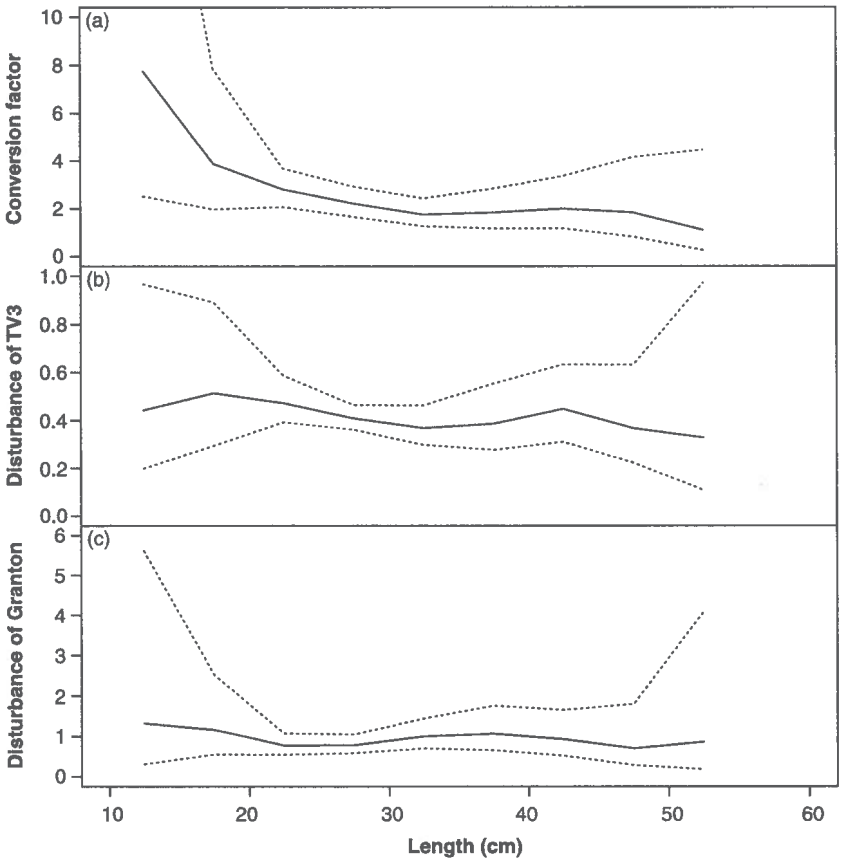
The paired hauls were made by conducting the vessel's second haul on the global positioning system track position line available from the first haul and in the same direction. The second haul was made immediately after the first, i.e., commenced within 0.75–1 h after the retrieval of the first haul. The duration of each haul was 30 min (±2 min) carried out with the same trawling speed of about 3 kn. The field experiments were restricted to the types 1–3, i.e., omitting trials replicating tows with the old gear (Table 2).

Before analysis, the catch data were standardized to 30-min haul duration and were grouped into 5-cm length groups (rounded numbers because the binomial distribution model applied demands integer values). A few haul pairs were ex-

Table 2. Number of Baltic Sea stations with paired hauls and average number of fish caught per station by type of experiment, gear, and length group.

	Average number of fish caught by type of experiment					
	Type 1 (old gear – new gear)		Type 2 (new gear – old gear)		Type 3 (new gear – new gear)	
Length group (midpoints) (cm)	Granton haul 1	TV3 haul 2	TV3 haul 1	Granton haul 2	TV3 haul 1	TV3 haul 2
12.5	0.9	9.8	15.7	0.9	12.2	5.3
17.5	8.9	39.5	30.0	4.1	15.8	8.1
22.5	41.3	90.6	55.7	9.2	161.9	76.9
27.5	90.4	157.3	47.8	8.9	299.4	122.8
32.5	38.9	68.6	51.5	11.0	137.1	50.6
37.5	15.5	30.5	41.3	8.6	47.6	18.1
42.5	10.6	20.0	19.5	4.5	43.0	19.6
47.5	6.7	8.6	7.5	1.5	23.8	8.6
52.5	2.8	2.7	3.5	1.0	6.6	2.1
No. of stations	24	28	8			

Fig. 1. Estimates (solid line) and 95% confidence limits (broken lines) by length of conversion factors for (*a*) Granton converted to TV3, (*b*) disturbance effects of the TV3 trawl, and (*c*) disturbance effects of the Granton trawl.



cluded from the analysis because that total number of fish caught per haul was especially low, less than 20 individuals. Cod less than 10 cm were not recruited fully to any of the gears and were therefore omitted from the analysis. Similarly, the largest cod, i.e., cod greater than 55 cm in length, were excluded from the analyses because of a low number of fish caught.

Results

The model eq. 9 was applied to the Danish comparative trawl experiment data. The estimated conversion factors show a clear decline with fish length from values above 9 for the smallest cod sizes to values between 1 and 2 for cod greater than 25 cm. (Fig. 1*a*). In contrast, for the disturbance

Table 3. Test results of hypotheses H_1–H_4 using Type3 analysis (SAS notation).

Test	df	χ^2 (Type3)	$P > \chi^2$
H_1: No overdispersion	490	1749	<0.0001
H_2: $\gamma_l = \gamma$	8	14.22	<0.0001
H_3: $\alpha_l = \alpha$	8	3.76	0.4391
H_4: $\beta_l = \beta$	8	4.77	0.7822

Table 4. Conversion factors, γ_l, and lower and upper confidence limits (CL) by length for the conversion of Granton catches to TV3 units.

Length (cm)	Conversion factor	Lower 95% CL	Upper 95% CL
12.5	9.19	4.93	17.12
17.5	4.17	3.21	5.43
22.5	2.46	2.06	2.95
>22.5	1.96	1.69	2.27

Table 5. Estimated disturbance parameters of the Granton trawl (α) and the TV3 trawl (β) and their lower and upper confidence limits (CL).

	Disturbance	Lower 95% CL	Upper 95% CL
α	0.90	0.77	1.05
β	0.42	0.38	0.46

factors (α_l and β_l), no clear systematic trends with cod size were observed (Figs. 1*b* and 1*c*).

Four hypotheses were tested:

H_1: No overdispersion

H_2: $\gamma_l = \gamma \Leftrightarrow \pi_l = \pi$

H_3: $\alpha_l = \alpha \Leftrightarrow \theta_l = \theta$

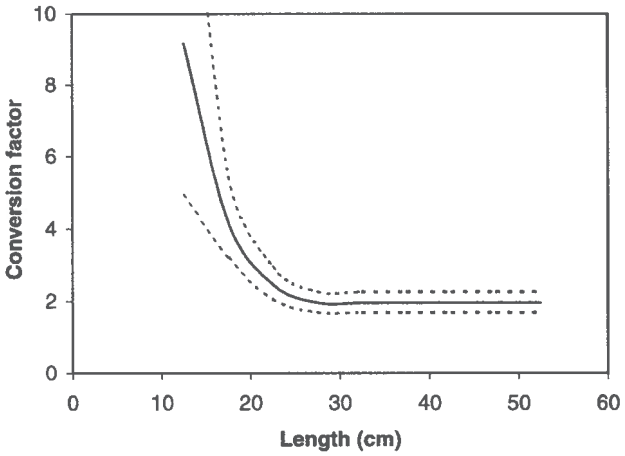
H_4: $\beta_l = \beta \Leftrightarrow \tau_l = \tau$

The dispersion was estimated at 1.89, which is significantly larger than 1, indicating that the conditional distribution considered is overdispersed compared with the binomial distribution assumed (Table 3). The tests of the hypotheses H_3 and H_4 were accepted and showed in both cases a clear independence of fish length (Table 3). However, the hypothesis H_2 that the conversion factors were the same for all length groups was rejected. The tests applied requires that the expected value of $U^{\text{seq}}_{\text{type},l,s}$ is larger than 5. This is the case for all length groups except for the largest fish larger than 50 cm. For the latter group, the results of the χ^2 test should be treated with caution.

To model the relationship between the conversion factors and length, the model eq. 9 was modified by expressing π_l as continuous variables in the form of a third-degree polynomial and by assuming the that disturbance factors are independent of fish size:

$$r_{\text{type},l} = (al^3 + bl^2 + cl + d)x_{\text{type}} + \theta y_{\text{type}} + \tau z_{\text{type}}$$

Fig. 2. Estimated conversion factors (solid line) and 95% confidence limits (broken lines) by length for Granton converted to TV3 using the final model (eq. 10).



Successive testing within this model showed that all coefficients of the polynomial of third degree were significant different from zero, which indicates that the conversion factor depends on the length. The estimated conversion factors, however, for fish larger than 25 cm were found to be very similar (Fig. 1*a*), and when removing fish less than 25 cm from the analysis, the hypothesis $a = b = c = 0$ was accepted, indicating that the conversion factor is the same for fish larger than 25 cm. For this reason, fish greater than 25 cm were aggregated into a single plus group. This led to the final model where the conversion factors differ for the four length classes, whereas both disturbance factors are independent of length:

$$r_{\text{type},l} = \pi_l x_{\text{type}} + \theta y_{\text{type}} + \tau z_{\text{type}}$$

for the length groups l = 12.5, 17.5, 22.5, and >25 cm.

In the final model, the conversion factor decreases from a value of approximately 9 for the smallest length class to a plateau of approximately 2 for fish greater than 25 cm (Fig. 2; Table 4). For none of the length classes does the confidence interval include the value of 1, implying that for all sizes of cod, the new trawl is significantly more efficient than the old trawl. The confidence limits are much wider for small fish of length 10–15 cm because of a low number of fish caught. Both disturbance parameters are independent of length. For the TV3 trawl, the disturbance factor is estimated at 0.42 and is found to be significantly different from 1, implying that fishing with this gear lowers the availability of cod in the short run. The disturbance factor for the Granton trawl is estimated at 0.90 and is not found to be statistically different from 1 (Table 5).

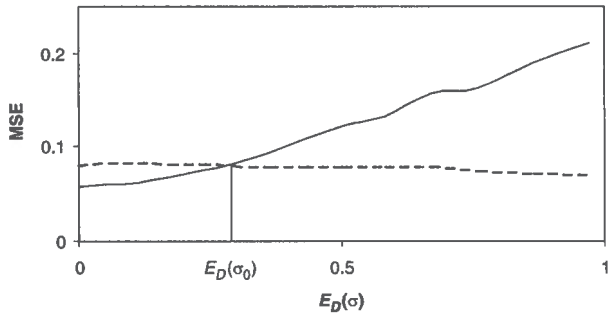
Simulation study

Simulation study 1, which assesses the relative bias and mean square error (MSE) of the estimators of the conversion factors associated with the new method (paired hauls taken in the same track lines), was carried out for two alternative estimators (the ML estimator $\hat{\gamma}_1$ used in the model and $\hat{\gamma}_2$ being the geometric mean over stations; see Appendix B). The bias and MSE were generally found to be very low ex-

Table 6. Relative bias and MSE of $\hat{\gamma}_1$ and $\hat{\gamma}_2$ by length group obtained from simulation study 1 (Appendix B).

	Relative bias		MSE	
Length group (midpoints) (cm)	$(\hat{\gamma}_1/\gamma - 1)$	$(\hat{\gamma}_2/\gamma - 1)$	$\hat{\gamma}_1$	$\hat{\gamma}_2$
12.5	0.16	–0.39	36.6	22.0
17.5	0.03	–0.18	1.5	2.11
22.5	0.01	–0.003	0.08	0.16
>22.5	0.003	–0.07	3×10^{-5}	0.02

Fig. 3. MSE of $\hat{\gamma}_1$ (new method: broken line) and $\hat{\gamma}_4$ (paired hauls: solid line) versus mean absolute value of relative deviation between fish densities at two parallel track lines, $E_D(\sigma)$, for the Atlantic cod size group 20–25 cm. At the intersection $E_D(\sigma_0)$, the two methods provide results of equal quality.



cept for the smallest fish size class where catches were low (Table 6). The MSE of $\hat{\gamma}_1$ was found to be less than the MSE of $\hat{\gamma}_2$ for all length groups except for the 12.5 cm group, i.e., for more than 99% of the fish caught with the old Granton trawl. For the 12.5 cm group, however, the bias of $\hat{\gamma}_2$ is more than double of that of $\hat{\gamma}_1$. Overall, we therefore conclude that the estimator $\hat{\gamma}_1$ is superior to $\hat{\gamma}_2$. As a consequence, estimator $\hat{\gamma}_1$ is used for the new method in simulation study 2.

Simulation study 2 was initiated by assessing the most efficient estimator of the conversion factor associated with the traditional paired hauls design. It was here found that the estimator $\hat{\gamma}_4$ was superior and $\hat{\gamma}_4$ was therefore used for that method (Appendix B).

The relationship between spatial inhomogeneity ($E_D(\sigma)$), which measures the relative difference between the density of the two paired hauls stations, and MSE of the two methods shows that the MSE of the new method ($\hat{\gamma}_1$) is approximately constant (i.e., independent of the fish distribution), while the MSE of the traditional paired hauls method ($\hat{\gamma}_4$) is an increasing function of the spatial inhomogeneity (Fig. 3 shows the results for the 20–25 cm length group). As the MSE of the paired hauls design is less than the MSE of the new method at complete spatial homogeneity, the two curves intersect at a point denoted $E_D(\sigma_0)$. When $E_D(\sigma) > E_D(\sigma_0)$, the new method is preferable and vice versa. The interception points ($E_D(\sigma_0)$) differ between the size classes of cod because of the difference in observed catches (Table 7).

The $E_D(\sigma_0)$ is about 30% for fish larger than 20 cm that accounted for 95% of the fish caught with the old and inefficient Granton trawl. For small fish, which were poorly represented in the Granton trawl catches, the interception point

Table 7. Comparison of the new method ($\hat{\gamma}_1$) with the paired hauls method ($\hat{\gamma}_4$) obtained from simulation study 2.

		Relative bias	
Length group (midpoints) (cm)	$E_D(\sigma_0) = E(\lvert D_1/D_2 - 1\rvert)$	$(\hat{\gamma}_1/\gamma - 1)$	$(\hat{\gamma}_4/\gamma - 1)$
12.5	4.50	0.10	–0.43
17.5	1.30	0.03	–0.17
22.5	0.30	0.01	0.03
>22.5	0.31	0.003	–0.02

Note: The mean absolute value $E_D(\sigma_0)$ of relative deviation between fish densities at two nearby hauls, D_1 and D_2, for which the MSE of the new method equals that of the paired hauls estimator $\hat{\gamma}_4$ and relative bias of the two estimators (see Appendix B).

Table 8. Ratio of the minimum variances of the conversion factors estimated by either type 2 + type 3 or type 0 + type 1 experiments when assuming equal effort ($m_{0+1} = m_{2+3}$).

Length group (cm)	$\frac{V^{\min}(\hat{\gamma}_{2+3})}{V^{\min}(\hat{\gamma}_{0+1})}$ *
12.5	0.91
17.5	1.02
22.5	1.17
>22.5	1.26

*Equation 12/eq. 13.

is much higher, 450% and 130% for length groups 12.5 and 17.5, respectively. However, the bias in the conversion factors associated with the traditional paired hauls design is substantial for the small size classes and significantly higher than found with the new method (Table 7).

Optimal survey design

Based on the conversion and disturbance factors estimated and assuming equal effort (i.e., $m_{0+1} = m_{2+3}$), the relationship between the variances determined by eqs. 12 and 13 has been calculated (Table 8). The strategy based on experiments of types 2 + 3 should be preferred if the relationship is less than 1. The table shows that that the differences between the two strategies are small. Strictly following the results, strategy 2 + 3 should be preferred for fish less than 15 cm, whereas strategy 0 + 1 should be preferred for the larger fish.

The calculation of the optimal design is based on the assumption of the binomial distribution. However, the analyses showed that the observations were overdispersed compared with the binomial distribution. The calculations provided should therefore be regarded as an approximation to the optimal design.

Discussion

There are a number of approaches available for estimating relative fishing powers between different vessels or gears. The approaches have different merits and faults and the selection of the most appropriate method will depend on the scientific scope, the resources available, and the peculiarities of the biological system studied. A major issue is the dis-

tinction between designated experiments and the use of existing data as available from scientific surveys or commercial catch rates (e.g., Robson 1966; Gavaris 1990; Sparholt and Tomkiewicz 2000). For the designated experiments, the paired hauls experimental design is an appealing approach when stations close in time and space are more similar than stations widely spaced. Wilderbuer et al. (1998) analysed survey data covering a wide depth range and found for that case that fishing power was more precisely estimated by the methods that explicitly used the paired hauls information available. However, a number of papers have demonstrated considerable spatial variability in catch rates between nearby stations (e.g., Ehrich 1991; Kvist et al. 2001), implying that nearby hauls do not cover the same population, which means that the benefits of paired nearby stations vanish. Further, in practice, information on the spatial distribution of the resource populations is rarely available.

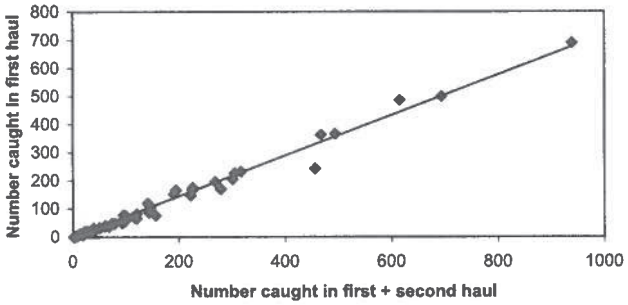
The key quality of the method developed here is that the gear comparisons are conducted at the same sites, implying that it is independent of the finer scale spatial distribution of the resources. It is assumed that density and size structure of the resource are retained at the station site within the short duration between successive tows except for the systematic and estimable disturbance effects caused by the fishing operations. The method has the additional merits in that it uses standard statistical techniques that allow maximum likelihood estimation of parameters, calculation of confidence limits of the estimates, and testing of hypotheses. The simulation studies additionally showed that the estimated conversion factors were practically unbiased for size groups that accounted for more than 99% of the fish caught.

For the traditional paired hauls comparisons, it is not possible to assess bias and uncertainties of the conversion factors because they depend on the fine-scale spatial distribution of the resources, which is not known.

For a special case of spatial distribution for which strict assumptions have to be fulfilled, we presume that it is possible to obtain the statistical properties of conversion factor estimates from a paired hauls design experiment by, e.g., Markov Chain Monte Carlo or Bayesian techniques. The assumptions are that the densities from nearby stations originated from the same statistical distribution and that the variance of the densities were equal across all stations fished. Simulations carried out for this case showed that increasing spatial inhomogeneity led to poorer performance of the traditional paired hauls method, whereas the new method was insensitive to the homogeneity differences. For the present Baltic Sea case, the simulations indicated that for the larger cod (accounting for 95% of the catch), the new method was preferable when the mean density difference between two paired stations exceeded 30%.

The new TV3 trawl was significantly more efficient than the Granton trawl hitherto used, especially for cod less than 20 cm. This is in line with the a priori expectations, as the new trawl was larger both vertically and horizontally and used a rubber snake ground gear instead of the bobbin arrangement used earlier. This new ground rope arrangement was suggested as the survey standard (ICES 1997), acknowledging the body of research that has documented the scope of enhancing the catchability of small cod owing to its ability to follow bottom (Engås and Godø 1989; Walsh 1989; Ehrich 1991).

Fig. 4. Number caught in the first haul versus number caught in the first haul plus the second haul by station and length group for type 3 experiments. The line shows the expected value based on the estimated β.



The analyses showed that the disturbance effect of the TV3 trawl was quite significant, being estimated at about 0.4, implying that the fish density available for the subsequent haul was reduced by 60%. Although the disturbance effect is not of primary interest when calibrating gear efficiency, its inclusion in the model crucially affects the estimated size of the conversion factors. This may be illustrated by contrasting the present approach with that used by Wilderbuer et al. (1998) who ignored the disturbance factors but attempted to balance out the sequence effect by splitting their survey effort equally between the type 2 and type 3 experiments. When using this approach, the conversion factor can be expressed as $\gamma = 0.5(\alpha + 1/\beta)(q_{new}/q_{old})$. Inserting the disturbance information available from the present study shows that by ignoring disturbance effects, the conversion factor would be overestimated by 64%.

The disturbance effect introduced here is conceptually related to the depletion effects known from population size estimation from consecutive fishing on a closed population (i.e., Leslie and deLury method used in freshwater fishing; cf. Ricker 1975). However, the disturbance effect designates a net effect that includes both the removal of fish caught by the first fishing operation and induced behavioural effects that influence migration of fish in the neighbourhood of the trawl track line. Because of the nonclosed nature of a trawl operation, it is impossible to distinguish between these two effects. The estimated disturbance parameters are nevertheless related to the size of the catch as reflected by the catchabilities. The disturbance effect of the relative inefficient Granton trawl was thus estimated at 0.90, which was not significantly different from 1.0, whereas the disturbance effect of the more efficient TV3 trawl was estimated at 0.4 and was clearly found to be significantly different from 1.0.

For the approach taken here, it is assumed that both disturbance effects and conversion factors depend only on the size of the fish but not on any station or habitat characteristics such as depth, fish abundance, or bottom type. Although the present experiments were not designed to illuminate the importance of station differences, a simple graphical evaluation of such possible effects was made by plotting CPUE for the first haul against the sum of CPUEs of the first and second hauls for the type 3 experiments (Fig. 4). According to the model, the observations from each station and length

class should lie around a line through the origin with a slope equal to $1/(1 + \beta_l) = 0.7$ as $\beta_l = \beta = 0.42$. No stations were found to be obvious outliers and no trends in residuals pattern by density were observed, indicating that the fish density did not influence the disturbance effect.

With the present model formulation, the estimates and the uncertainty of the parameters depend only on the number of fish caught and not on the number or type of stations covered, implying that if it is possible to catch a high number of fish at a few stations, this should be sufficient to obtain suitable conversion factors. However, it cannot be precluded that systematic station differences may imply that catchability and disturbance differ across habitats, and if such factors are identified as important, the experimental design and the model should be changed accordingly, e.g., by including the factor in the generalized linear model (eq. 9).

The section on survey design notes that for the present model, the conversion factors can be estimated by carrying out either type 2 (new gear – old gear) and type 3 (new gear – new gear) experiments or type 0 (old gear – old gear) and type 1 (old gear – new gear) experiments.

When prior information on conversion and disturbance factors is available, which is the case when the experimental hauls are not restricted to a single survey, the precision of gear conversion estimates for the two alternatives may be evaluated, enabling the researcher to choose the optimal survey design. Within the strategy chosen, the researcher may subsequently choose the optimum allocation of hauls between the two types of experiments involved. Furthermore, for a specified level of uncertainty associated with the conversion factors estimated, the number of paired stations required can be determined.

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Appendix A

In some cases, observations of type 0 (paired replications using the old trawl) are not available because it is not obvious if they are necessary to estimate conversion factors. Therefore, if it is assumed that only observations for types 1, 2, and 3 are available, the likelihood function for a given length group l is a product of three binomial distributions:

$$L_l((C_{t,l,s}|U_{t,l,s})) = \prod_{t=1}^{3}\prod_{s}\binom{U_{t,l,s}}{C_{t,l,s}} p_{t,l}^{C_{t,l,s}}(1-p_{t,l})^{U_{t,l,s}-C_{t,l,s}}$$

where $C_{1,l,s} = U^2_{1,l,s}$, $C_{t,l,s} = U^1_{t,l,s}$, and $t = 2, 3$ and $p_{t,l}$, $t = 1, 2, 3$, is defined by eqs. 6–8.

It can be shown that the maximum likelihood estimates of the parameters are

$$\text{(A1)}\quad \hat{\beta}_l = \frac{1-\hat{p}_{3,l}}{\hat{p}_{3,l}} = \frac{\sum_s U^2_{3,l,s}}{\sum_s U^1_{3,l,s}}$$

$$\text{(A2)}\quad \hat{\gamma}_l = \hat{\beta}_l \frac{\hat{p}_{2,l}}{(1-\hat{p}_{2,l})} = \hat{\beta}_l \frac{\sum_s U^1_{2,l,s}}{\sum_s U^2_{2,l,s}}$$

$$\text{(A3)}\quad \hat{\alpha}_l = \frac{1}{\hat{\gamma}_l}\frac{\hat{p}_{1,l}}{(1-\hat{p}_{1,l})} = \frac{1}{\hat{\gamma}_l}\frac{\sum_s U^1_{1,l,s}}{\sum_s U^2_{1,l,s}}$$

where

$$\text{(A4)}\quad \hat{p}_{t,l} = \frac{\sum_s C_{t,l,s}}{\sum_s U_{t,l,s}}$$

Equations A1 and A2 show that the estimated disturbance parameter $\hat{\beta}_l$ solely depends on the type 3 experiments, whereas the estimated conversion factor $\hat{\gamma}_l$ solely depends on the experiments of types 2 and 3 (and not type 1). This means that when experiments of types 1, 2, and 3 are available, the type 1 experiments do not contain information on the conversion factor but only information on the disturbance parameter α_l. However, if type 0 experiments were available, data from all four experiments would contribute to the estimation of all three parameters.

In situations where the disturbance effect of the old gear, α_l, is the same for some length groups, eqs. A1–A3 do not hold and the estimates of γ_l depend on observations from all three types of experiments.

Appendix B. Simulation studies

Study 1. Investigation of the bias of the new method and comparison with an alternative estimator

In this study, it is assumed that for each station the catch simulations are based on the same fish density such that only the generated catches vary in the simulations. All simulations were carried out for each of the length groups separately and were based on the observed 28 type 2 and 8 type 3 to match the current observations. The length groups for the large fish were aggregated as in the analyses. The simulations were based on the parameters estimated to reflect the empirical observations.

First, the fish densities for a given length group at each station were generated. The (unknown) catchability of the new gear, $q_{\text{new},l}$, was arbitrarily set to 0.5. The densities at each station during the first haul were calculated by $D_{t,l,s} = u^1_{t,l,s}/q_{\text{new},l}$, where $u^1_{t,l,s}$ is the observed CPUE and $t = 2, 3$, which ensures that the observed relative density distribution is applied. The catchability of the old gear was calculated by $q_{\text{old},l} = q_{\text{new},l}/\gamma_l$. The initial choice of $q_{\text{new},l}$ does not affect the analyses, as the CPUE data simulated are the same irrespective of the chosen catchability.

CPUE was assumed to follow a negative binominal (NB) distribution to reflect that the observed conditional distributions, $U^1_{t,l,s}|u_{t,l,s}$, were overdispersed compared with the binomial distribution. Accordingly, it was assumed that

$$\text{(B1)}\quad U^1_{t,l,s} \sim \text{NB}\left(q_{\text{new}} D_{t,l,s}\frac{p}{(1-p)}, p\right),\ t = 2, 3$$

$$\text{(B2)}\quad U^2_{t=2,l,s} \sim \text{NB}\left(\beta q_{\text{old}} D_{t=2,l,s}\frac{p}{(1-p)}, p\right)$$

$$\text{(B3)}\quad U^2_{t=3,l,s} \sim \text{NB}\left(\beta q_{\text{new}} D_{t=3,l,s}\frac{p}{(1-p)}, p\right)$$

This parameterization implies that $E(U^1_{t,l,s}) = q_{\text{new}} D_{t,l,s}$, $E(U^2_{t=2,l,s}) = \beta\, q_{\text{old}} D_{t=2,l,s}$, and $E(U^2_{t=3,l,s}) = \beta\, q_{\text{new}} D_{t=3,l,s}$, and that $\text{VAR}(U^i_{t,l,s}) = E(U^i_{t,l,s})/p$, $i = 1, 2$. According to the last equation, $1/p$ denotes the overdispersion in the NB distribution compared with the Poisson distribution. The parameter p has been chosen such that $1/p$ equals the overdispersion of $U^1_{t,l,s}|U_{t,l,s}$ compared with the binomial distribution found in the analyses (see Appendix C).

For each length group, station, and type of experiment, 10 000 set of pairs of CPUEs, $U^1_{t,l,s}(i), U^2_{t,l,s}(i))$, $i = 1,...,10\,000$, were randomly drawn from the NB distributions B1–B3. For each simulation, the conversion factor was estimated by the maximum likelihood estimator

$$\text{(B4)}\quad \hat{\gamma}_{1,l}(i) = \frac{\sum_s U^2_{3,l,s}(i)\sum_s U^1_{2,l,s}(i)}{\sum_s U^1_{3,l,s}(i)\sum_s U^2_{2,l,s}(i)}$$

using eqs. A1 and A2 in Appendix A.

An alternative estimator based on geometric averages, $\hat{\gamma}_{2,l}(i)$, was considered as well:

$$\hat{\gamma}_{2,l}(i) = \left(\frac{U^2_{3,l,1}(i)}{U^1_{3,l,1}(i)} \times \ldots \times \frac{U^2_{3,l,T}(i)}{U^1_{3,l,T}(i)}\right)^{1/T} \times \left(\frac{U^2_{2,l,1}(i)}{U^1_{2,l,1}(i)} \times \ldots \times \frac{U^2_{2,l,S}(i)}{U^1_{2,l,S}(i)}\right)^{1/S}$$

where S and T are the number of type 2 and type 3 stations, respectively.

The estimators have been compared using the relative bias $\gamma_{j,l}/\gamma_l - 1$ and the mean squared error $\text{MSE} = E(\hat{\gamma}_{j,l} - \gamma_l)^2 = \text{bias}^2 + \text{VAR}(\hat{\gamma}_{j,l})$ as measures of the goodness of the estimators, where γ_l are the assumed true values estimated. The mean of the two estimators has been estimated by $\hat{\gamma}_{j,l} = \frac{1}{10\,000}\sum_{i=1}^{10\,000}\hat{\gamma}_{j,l}(i)$, the relative bias by $\hat{\gamma}_{j,l}/\gamma_l - 1$, and MSE by

$$\hat{\text{MSE}}_{j,l} = \frac{1}{10\,000}\sum_{i=1}^{10\,000}(\hat{\gamma}_{j,l}(i) - \gamma_l)^2 \text{ for } j = 1, 2$$

Study 2. A case-specific comparison of the new method and the paired hauls design

The assumption in this study is that the fish densities at each paired nearby station originate from the same statistical

distribution. The number of paired stations was the same as in simulation study 1, namely 28 type 2 and 8 type 3 experiments, i.e., 36 in total.

Let $D_l = \{D_{t=2,l,s=1}, \ldots, D_{t=2,l,s=28}, D_{t=3,l,s=1}, \ldots, D_{t=3,l,s=8}\}$ denote the combined set of the same (mean) densities as calculated in the first simulation experiment and let $D_{l,u}$, $u = 1,\ldots, 36$, denote the uth element. For each length group, the two fish densities at each of the paired stations, $D^1_{l,u}$ and $D^2_{l,u}$, were generated assuming that they both originated from the same lognormal distribution. The new gear was applied to the stations with densities $D^1_{l,u}$, while the old gear was applied to $D^2_{l,u}$.

For the paired hauls design, we do not distinguish between type 2 and type 3 experiments such that CPUEs for the new and old gears, $U^1_{l,u}$ and $V^2_{l,u}$, respectively, were generated based on densities $D^1_{l,u}$ and $D^2_{l,u}$ for $u = 1,\ldots, 36$.

For the new method, we distinguish between type 2 and type 3 experiments. This means that only the stations fished by new gear and the corresponding CPUEs, $U^1_{t,l,s}$, were used in the simulations as the first haul taken in both type 2 and type 3 experiments. The CPUEs from the second haul, $U^2_{t,l,s}$, were generated accounting for the disturbance effect.

The catchabilities and conversion factors used were similar to those in simulation study 1. For a given length group l, the simulation procedure was as follows.

1. Let σ and length group l be specified.
2. $i = 1$.
3. Generate densities $D^1_l(i) = \{D^1_{l,1}(i), \ldots, D^1_{l,36}(i)\}$ and $D^2_l(i) = \{D^2_{l,1}(i), \ldots, D^2_{l,36}(i)\}$ from the lognormal distributions $\{\mathrm{LN}(\ln(D_{l,1}), \sigma), \ldots, \mathrm{LN}(\ln(D_{l,36}), \sigma)\}$.
4. Generate CPUEs

$$U^1_{l,u}(i) \sim \mathrm{NB}(q_{\mathrm{new}} D^1_{l,u}(i) \frac{p}{1-p}, p),\ u = 1,\ldots, 36$$

$$V^2_{l,u}(i) \sim \mathrm{NB}(q_{\mathrm{old}} D^2_{l,u}(i) \frac{p}{1-p}, p),\ u = 1,\ldots, 36$$

For the new method, the CPUEs from the second hauls, $U^2_{t,l,s}$, were generated according to eqs. B2 and B3 in simulation study 1:

$$U^2_{t=2,l,s} \sim \mathrm{NB}(\beta q_{\mathrm{old}} D^1_{l,u} \frac{p}{1-p}, p),\ u = 1,\ldots, 28$$

$$U^2_{t=3,l,s} \sim \mathrm{NB}(\beta q_{\mathrm{new}} D^1_{l,u} \frac{p}{1-p}, p),\ u = 29,\ldots, 26$$

5. Calculate the estimators of the conversion factor $\hat{\gamma}_{1,t}(i)$ for the new method using eq. B4. For the paired hauls design, three estimators were considered:

$$\hat{\gamma}_{3,l}(i) = \frac{\sum_{u=1}^{36} U^1_{l,u}(i)}{\sum_{u=1}^{36} U^2_{l,u}(i)}$$

$$\hat{\gamma}_{4,l}(i) = \left(\frac{U^1_{l,1}(i)}{U^2_{l,1}(i)} \times \ldots \times \frac{U^1_{l,36}(i)}{U^2_{l,36}(i)}\right)^{\frac{1}{36}}$$

$$\hat{\gamma}_{5,l}(i) = \frac{1}{36} \sum_{u=1}^{36} \frac{U^1_{l,u}(i)}{U^2_{l,u}(i)}$$

6. If $i < 10\,000$, $i = i + 1$, go to 3; otherwise stop.

Contrary to simulation study 1, both densities and catches by station were assumed to vary stochastically each time a simulation experiment was performed. This procedure ensured that the effect of density variations by station was included. Relative bias and MSE of the estimators were calculated as in simulation study 1.

The variability of fish density at the paired stations is described by the standard deviation σ, which approximately is the coefficient of variation of the densities. Obviously, the variability increases when σ increases. When $\sigma = 0$ (no variability between nearby stations), all paired hauls provide information useful to estimate γ, whereas in the new design, some effort is "wasted" on estimating the disturbance β. For this case, therefore, the paired hauls design is expected to be superior to the new method. However, the MSE of the paired hauls estimates is expected to increase when σ increases. In contrast, the conversion factor derived from the new method ($\hat{\gamma}_1$) is independent of density. However, as the density by station also varies stochastically for the new design, a slight trend in $\hat{\gamma}_1$ appears in the simulations. In general, it is expected that the two MSE curves intersect for one particular value of standard deviation denoted $\sigma_{0,l}$, as illustrated in Fig. 3. When σ_l is less than $\sigma_{0,l}$, the paired hauls design should be preferred, and when σ_l is larger than $\sigma_{0,l}$, the new method should be preferred. $\sigma_{0,l}$ has been calculated for $\hat{\gamma}_1$ and $\hat{\gamma}_4$ (the two best estimators) for each length group together with the relative bias of the estimators.

Instead of using the log variance, σ, that is input to the simulation study, we have chosen to express the variability by the absolute relative difference between two densities from paired stations, $E_D(\sigma) = E(|D^1_{l,u}/D^2_{l,u} - 1|)$, as this scale is believed to be more interpretable for survey scientists. $E_D(\sigma)$ only depends on σ and it can be shown that

$$E_D(\sigma) = \frac{2}{\sqrt{\pi}} e^{\sigma^2} \int_0^{\sigma} e^{-t^2} dt$$

which is a strictly increasing function of σ.

Appendix C. Determination of the overdispersion parameter in the negative binomial distribution

Consider a given length group and type 2 respective 3 experiments. For convenience, the indices for l and t have been left out. Again let U^i_s be the paired CPUEs for station s and assume that they are distributed as $\mathrm{NB}(\nu^i_s, p)$, $i = 1, 2$, where

$$\nu^1_s = q_{\mathrm{new}} D_s \frac{1-p}{p}$$

and

$$\nu^2_s = \beta q_{\mathrm{new}} D_s \frac{1-p}{p}$$

We know that the conditional distribution $U^1|U$ is beta-binomial (McCullagh and Nelder 1989) with parameters v^1 and v where

$$U^i = \sum_s U_s^i,\ U = U^1 + U^2$$

$$v^i = \sum_s v_s^i,\ i = 1, 2$$

and $v = v^1 + v^2$. The distribution is independent of p. The mean and variance of this distribution are

$$E(U^1|U) = U\frac{v^1}{v}$$

and

$$\mathrm{VAR}(U^1|U) = U\frac{v^1}{v}\left(1-\frac{v^1}{v}\right)\left(1+\frac{U-1}{v+1}\right)$$

The variance equation shows that the variance equals the binomial variance multiplied by the overdispersion term od:

$$\text{(C1)}\quad \mathrm{od} = 1+\frac{U-1}{v+1}$$

The present analysis indicates that the distribution of $U^1|U$ is overdispersed. From the estimated value of od, we then want to calculate the parameter p for the original variables U^1 and U^2. In principle, this is impossible because the beta-binomial is independent of p. However, as U is NB(v, p), $E(U) = v\frac{1-p}{p}$ or $\frac{1}{p} = 1+\frac{E(U)}{v}$. Inserting $v = \frac{U-\mathrm{od}}{\mathrm{od}-1}$ obtained from eq. C1, we get

$$\frac{1}{p} = \frac{\mathrm{od}\frac{E(U)-1}{U}+1-\frac{E(U)}{U}}{1-\frac{\mathrm{od}}{U}}$$

As U and $E(U)$ are large values compared with 1 and od, we approximately get

$$\text{(C2)}\quad \frac{1}{p} = \frac{E(U)}{U}(\mathrm{od}-1)+1$$

Equation C2 shows that

$$\frac{1}{p}\begin{cases} < \mathrm{od} & \text{for } U > E(U) \\ = \mathrm{od} & \text{for } U = E(U) \\ > \mathrm{od} & \text{for } U < E(U) \end{cases}$$

As $U = E(U)$ is close to the modus of the distribution of U with the largest probability, p was set to $\frac{1}{\mathrm{od}}$. However, the overdispersion in practise can be both smaller and larger than od.

Appendix references

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Chapter 3

Improving coupled hydro-acoustic and trawl research survey detection and survey efficiency

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Hydroacoustic *ex situ* target strength measurements on juvenile cod (*Gadus morhua* L.)

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Nielsen, J. R. and Lundgren, B. 1999. Hydroacoustic *ex situ* target strength measurements on juvenile cod (*Gadus morhua* L.). – ICES Journal of Marine Science, 56: 627–639.

Most TS-measurements on fish have been carried out for 38 kHz, and the existing TS algorithm for 120 kHz on cod is based on measurements on stunned fish. The main objective of these experiments was to establish an empirical estimate of the relation between acoustic reflection (target strength, TS) and length of live juvenile cod (7–10 cm and 15–20 cm) at 120 kHz. This was done by recording the variation in TS of freely swimming cod tracking single fish targets for the two size groups within the acoustic beam field. The experiment was set up in an open air 2000 m^3 tank where the small 5–10 cm long fish were swimming freely during measurement in cages (1 × 1 × 3 m) within the acoustic beam under natural conditions in seawater with a salinity of 30 and a temperature of 11°C. An EY500 split-beam acoustic system was used to detect single fish passing through the acoustic beam field, which was video recorded in order to isolate the measurements on single targets and to get an indication of their angle. A mean target strength-to-size relation was calculated for small cod based on single fish tracks with total acoustic angles below 3.5° off axis in the beam field. This relationship is compared to other TS measurements on juvenile cod in literature. TS at 120 kHz for the investigated cod size range seems to decrease faster by length than the 20 logL relation used for larger cod. The results were used to check the expected range limits of TS for juvenile cod during survey, and are expected to be taken into consideration in density estimation of juvenile cod during acoustic surveys targeting young gadoids in general.

Key words: *ex situ* target strength (TS) detection, *ex situ* TS experimental design and setup, metamorphosed juvenile cod, single fish tracks, split-beam hydroacoustics, TS to size equation.

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Introduction

There is no well-established TS-to-size relation for 120 kHz for live, free swimming juvenile cod (*Gadus morhua*, L.). The established 38 and 120 kHz TS algorithms for gadoids and clupeoids are mainly based on measurements on larger specimens. The main objective of the present *ex situ* experiments was to make an empirical estimate of the relation between target strength and length of juvenile cod at 120 kHz and to estimate the variation in the single fish TS for live, free swimming fish under natural oceanic conditions by tracking single fish targets within the acoustic beam field. The EY500 120 kHz split-beam system used is the same as used in association with the hydroacoustic field studies related to cod recruitment mechanisms in the Central Baltic Sea under the EU AIR Baltic CORE programme which includes hydroacoustic young fish surveys directed towards juvenile cod (Nielsen *et al.*, 1997). The present study was started because it has so far been difficult to obtain sufficiently disperse single-species occurrences of juvenile cod in relevant size groups optimal for *in situ* single fish TS estimations during these surveys. The catches of small cod were almost always mixed with sprat and small herring (Nielsen *et al.*, 1997). The empirical TS estimate obtained here has been used to check if the TS-data obtained during the survey are within the expected range

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limits for juvenile cod. Moreover the estimates of the TS–length-relationship from this study are expected to be of interest in general in acoustic abundance estimations of gadoids such as those successfully being conducted for the cod in e.g. the Barents Sea (Godø *et al.*, 1982; Hylen *et al.*, 1986; Godø, 1989; Godø and Wespestad, 1993), even though *ex situ* TS values are never fully representative for those at sea.

Materials and methods

Choice of the *ex situ* method to measure juvenile cod TS

The basic TS (Target Strength) relation, where the target strength is expressed in decibels (dB) as the ratio of reflected acoustic intensity from a given target to the incident intensity, is given by:

$$TS = 10 \log_{10}(\sigma/4\pi) = 10 \log_{10}(I_1/I_0) \quad (1)$$

where σ is the acoustic cross-section of the target, and I_1 and I_0 are the reflected and incident intensities (MacLKennan and Simmonds, 1992). As TS is used to convert area backscattering coefficient, Sa, to fish biomass, an accurate determination of TS is necessary. The methods used to estimate TS can be categorized as either *ex situ* or *in situ* and have been reviewed by MacLennan and Simmonds (1992) as well as Foote (1991). Most often the *ex situ* method has involved measuring TS of caged fish of known lengths and weights. In this way several biological and behavioural characteristics such as species, size class, tilt angle, directivity pattern, swimming speed, fish maturity, depth adaptation, and sometimes also swimbladder characteristics of the fish under study are known (e.g. Foote, 1987; Edwards *et al.*, 1984). The tilt angles of fish in experiments should ideally reflect the tilt angles found at sea. However the method can have the disadvantage of constraining the fish and the cages may restrict swimming and natural behaviour, consequently affect tilt angle, which in turn will affect TS to an unknown degree (Nakken and Olsen, 1977). Because TS varies strongly with tilt angle it is necessary to take variations in tilt angle into account either by measuring it directly or, as here, to estimate a mean of the measured TS values for some period with varying swimming behaviour.

In spite of the risk of unnatural conditions influencing the *ex situ* method, this method was chosen in the present study because of the inherent problems in getting well-defined conditions when measuring *in situ*. Major problems are: unknown tilt angle in relation to vertical migrations (e.g. MacLennan and Simmonds, 1992; Arnold and Greer Walker, 1992; Clay and Castonguay, 1996), unknown changes in swimbladder shape because of compression or decompression and unknown changes in tilt angle when a fish is not neutrally buoyant because it has changed depth quickly during vertical migration (Arnold and Greer Walker, 1992; Clay and Castonguay, 1996), unknown fishing-gear selection effects (e.g. Engås, 1991; Godø, 1990; Godø and Wespestad, 1993; Fernø and Olsen, 1994; MacLennan, 1992; MacLennan and Simmonds, 1992; Clay and Castonguay, 1996; MacLennan and Menz, 1996), no possibility of matching specific single fish echoes with corresponding single fish in the catch by length because juvenile fish in nature seldom occur in unimodal patches (MacLennan and Simmonds, 1992; MacLennan and Menz, 1996) and, finally, the risk of detecting multiple targets as single fish targets which is especially a problem for schooling fish (e.g. MacLennan and Menz, 1996; Rose, 1992; Wardle, 1983).

Choice of echosounder frequency in the experiments

Since measurements of this kind are performed on swimbladder fish it is expected that the targets resemble gas bubbles (Foote, 1980). For gas bubbles there is one resonance near the high-frequency limit of the Rayleigh scattering region (MacLennan and Simmonds, 1992, p. 31). A frequency of 120 kHz ($\lambda = 1.25$ cm) has been used in the present study ($L/\lambda \gg 1$), as well as during survey in the Baltic Sea, in an attempt to obtain linearity in the TS–size relations for juvenile cod, i.e. to minimize possible problems with the TS relationship caused by measuring in the Rayleigh region or in the resonance region of the bubble response curve. At intermediate sizes of the order of a wavelength where the dimensions of the physical (target) cross-section and the wavelength are similar, L/λ approaching 1, the scattered intensity increases rapidly to a peak at the resonance frequency of the bubble. At higher frequencies in the geometric region the frequency dependence of scattering strength of the gas bubble is small. Foote's (1987) TS relation for 38 kHz is valid for larger cod where the swimbladder size/wavelength relationship ($=L/\lambda$) is high ($\gg 1$). However this is not necessarily the case for small cod where the L/λ relationship is around or below 1. At 38 kHz λ is about 4 cm in sea water. When L/λ lies around 1 resonance might occur giving too large TS values for small cod. For L/λ smaller than 1 the acoustic cross-section area may decrease faster than the physical (target) cross-section area.

The maximum depth in the part of the central Baltic Sea where the field measurements on juvenile cod were performed does not exceed 100 m, and juvenile cod (<10–20 cm) has only been found in depths down to 90 m here (Nielsen *et al.*, 1997). Furthermore the absorption of sound in the Baltic brackish water is significantly lower than for oceanic water. Consequently the 120 kHz echosounder can cover the whole water

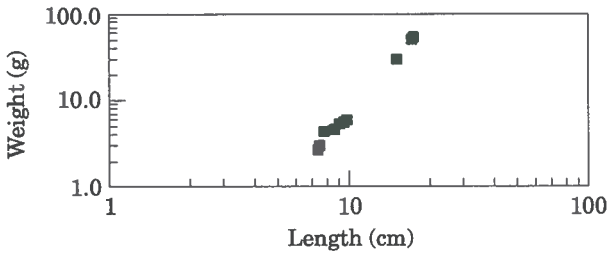

Figure 1. Size of the juvenile cod used in the experiments. Total length (mm) vs. wet weight (g) are shown on logarithmic scales.

column where juvenile cod occur in the survey area within its maximum reach.

Experimental facilities and materials

The *ex situ* measurements of TS on live juvenile cod were conducted in the period 2–11 October 1996. Measurements were made on two size groups of juvenile cod: one group consisting of seven 0-group cod of size 75–98 mm TTL (Total Tail Length) and another group consisting of three larger cod of size 159–188 mm TTL, respectively (Fig. 1). The cod used in the experiment were wild Skagerrak cod (ICES Subdivision IIIa) caught nearshore with beach seines in late September 1996. Because of relatively low sea temperatures in the summer of 1996, a consequence of the cold winter and spring, it was not possible to catch juvenile cod in suitable size groups nearshore until September. The experiments were conducted in a 2000 m^3, open air, concrete tank with a depth of 5 m and a diameter of approximately 22 m which is located at the North Sea Centre, Denmark. During the experiments concurrent TS measurements and video filming of the target volumes were performed in a net cage set up in the tank for several hours in daylight conditions each experimental day. The approach in the experimental design and set-up was to allow the fish to swim freely with some degree of natural schooling behaviour under natural physical conditions, and at the same time minimize acoustic reflections from the concrete tank walls, bottom, and centre pillar, as well as reflections from or signal reduction by the experimental set-up itself, especially the net cages and their attachments.

Experimental design and set-up in the experimental tank

The experimental set-up is outlined in Figure 2. On top of the tank is a bridge connecting the centre pillar with the tank sides. The bridge can be rotated all around the tank perimeter. On the bridge the transducer and video camera were mounted on special rigs that allowed the equipment to be placed at any suitable position in the water volume outside the net cages.

Three specially constructed net cages two of which are rectangular (1 m high × 1 m wide × 3 m long) and one trapeze shaped (the same dimensions as the rectangular cages but diminished by 5 cm on one vertical side) were made for the experiments. Three sides of the cages consisted of stiff monofilament polyethylene net with mesh size 2 mm and the fourth side was a transparent polyethylene window. Each end of the cages was stretched out by four polyethylene ribs 1 cm in diameter. Only one cage at a time was used in the experiment. The cage was held up and stretched out by 1.0 mm monofilament nylon lines, styrofoam floats, and sinkers on the cage, and anchors along the edge of the tank (Fig. 2). This system made it possible to manoeuvre and place the cage in whatever position and depth was needed to obtain optimal target reflection conditions and to minimize unwanted reflections. By hoisting the anchors the net cage could be taken to the surface to facilitate fish release and fish capture in the cage between the experiments. During an experiment the net cage was placed centrally between the centre pillar and the tank wall and typically in the middle of the vertical water column with its bottom 1–2 m above the tank bottom. The experiments were monitored and controlled from a small dry laboratory with a large (1.5 × 0.5 m) observation window into the tank.

Set-up of the echosounder system

The TS measurements were conducted with a portable SIMRAD EY500 120 kHz split-beam echosounder system with version 5.0 software (SIMRAD, 1996a). The transceiver in the dry lab was connected to an ES120-7 split-beam type with a 3 dB nominal beamwidth of 7° on the rig (Fig. 2).

The echosounder system was calibrated in the tank using the standard target method (Foote *et al.*, 1986; Degnbol, 1988; Degnbol *et al.*, 1990) with a 30.5 mm diameter copper sphere under conditions similar to the experimental conditions. The target distance was approximately 2.5–3.0 m. Echosounder settings during experiments and calibration were the following: ping interval ~8 pings s^{-1}, TVG 40 logR, pulse length medium (0.3 ms), bandwidth wide, absorption coefficient 0.038 dB m^{-1}, two-way beam angle (directivity) −20.4 dB. The resulting calibration values from the Simrad LOBE calibration program were: TS transducer gain 27.1 dB, 3 dB beamwidth of 6.4° and 6.3° (T=19°) for alongships and athwartships directions, respectively, alongships offset 0.09°, athwartships offset −0.32°. Other parameter settings for the EY500 system during experiments were the following: minimum value for TS-detection −60 dB, minimum echo length 0.8, maximum echo length 1.5, maximum gain compensation 4.0 dB, maximum phase deviation 4.0.

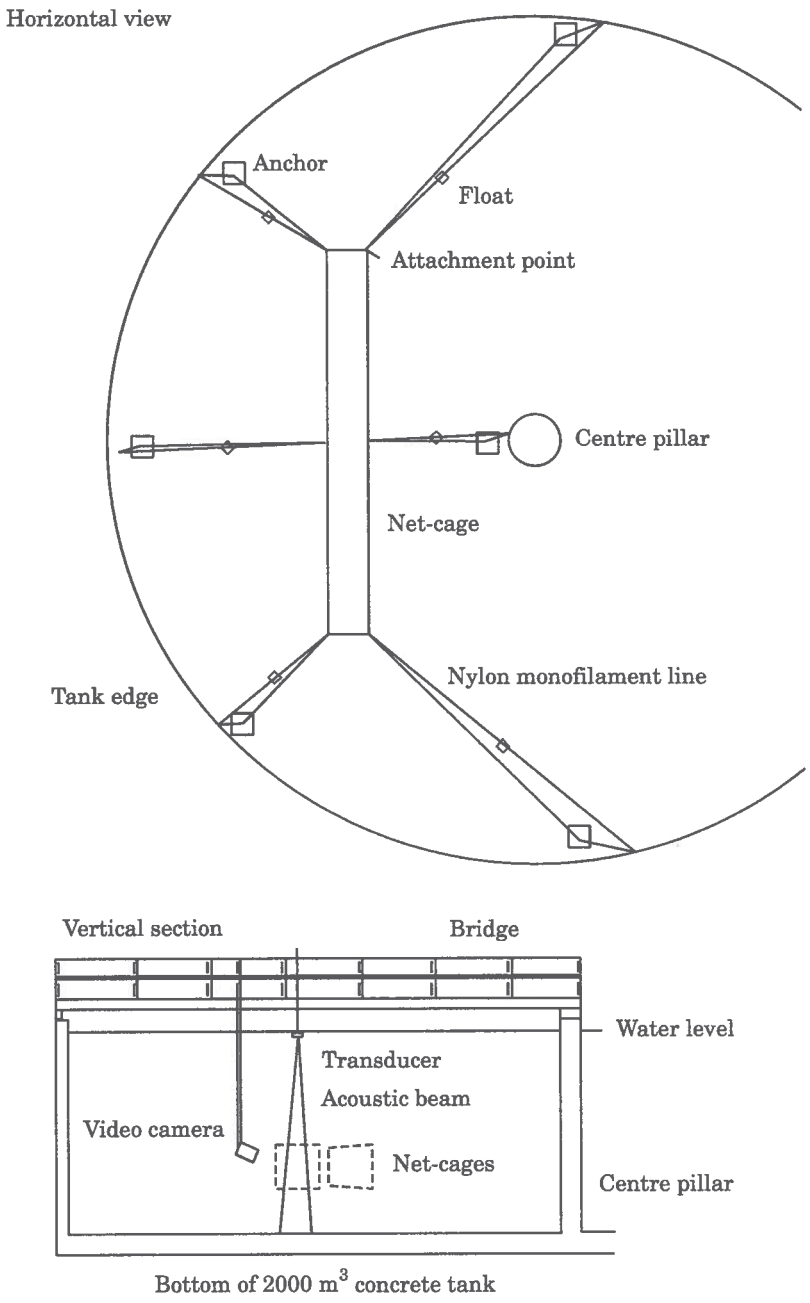

Figure 2. Schematic overview of the experimental set-up in the 2000 m^3 concrete tank.

The selection of minimum TS-thresholds on −60 dB was based on several replays in the EY500 software, as raw data had been sampled, where also lower levels of minimum TS thresholds were tested (−65 dB and −70 dB). No measurements in any of the tracks in any of these runs for the smaller group of juvenile cod showed lower TS values than −59 dB found for the smaller group of cod, and the TS variation in the single tracks did not change. This threshold also avoided noise from plankton organisms which also could be tracked when using a lower minimum threshold. The TS measurements were made using medium pulse length and wide bandwidth related to the small depth and the narrow range over which the measurements have been performed. With short pulse length the data would have had a better depth resolution, but this would have resulted in only few samples over depth resulting in badly defined mean angles and single echo selections (Soule *et al.*, 1997). A long pulse length would be of the same magnitude as the cage height and, consequently, would not be optimal.

With the above transducer parameters, and a typical placement of the cage-top at 2.2 m below the transducer, the beam is about 25 cm wide at the top of the cage and about 35 cm at its bottom, well below the width of the cage. The range of the sampling layer was 0.7 m with a range starting between 2.6 and 2.8 m. The distance of target measurement was between 2.79 and 3.21 m (Table 1) which was outside the near-beam field of the transducer, and assured that possible risks of interference effects were insignificant. The active diameter of the ES120-7 transducer is 107 mm. The near field range of the transducer is d^2/λ, where λ is 1500/120=12.5 mm (=sound speed in water/frequency), and consequently $107^2/12.5=916$ mm. SIMRAD specifies a distance of twice the near-field range as the critical working range, i.e. 1.83 m. Thus, the present measurements are made well within the far field of the transducer (H. Bodholt, SIMRAD, Norway, pers. comm.). The calibration of the transducer showed no obvious problems with variability in TS of the copper sphere.

In the experiment the magnitude of the reflection noise (ringing) from the tank wall, bottom, and centre pillar, and also acoustic reflection noise from the experimental set-up (cages, anchors, weights, floaters, monofilament lines, etc.) were checked. Most of this type of noise was at least 20 dB below the echo levels of the targets of interest when the ping rate was kept below 8 pings s^{-1}. The signal level of the reflections from the top of the net cage was of the same order of magnitude as the fish echoes. The acoustic damping by the upper side of the net cage was checked by lowering a spherical target through a small hole in the upper side of the cage and was found to be less than 0.3 dB. Only the reflection from the vertical cage sides could disturb the measurements but accurate positioning of the acoustic transducer avoided these reflections so only echoes from the top and bottom were visible. To remove gas bubbles both the upper side of the net cage and the transducer surface were treated with dilute soap solution before each experiment and checked regularly.

Setup of the video recording system

In order to make it possible to monitor the number of fish in the acoustic beam, and to have some indication of their swimming direction and body tilt, a video recording system (ROS Nuclear Products Division) was used. The position of the camera in the experimental setup is shown in Figure 2. The system includes an underwater, environmental colour TV camera unit with a 6-to-1 zoom lens and with a complete remote control of pan and tilt, zoom, focus, and iris. The video monitor connected to the recorder and the camera makes it possible to view the images while both recording and replaying. A PC was connected by a special interface to the remote control connector of the video recorder in order to acquire the tape counter data as a function of time for synchronization with the acoustic data.

Progress and sequence of tank experiments

Immediately before the experimental period the wild juvenile cod were transferred to an open, fish-holding jar system. They were kept in a flow of Skagerrak sea water for some days so that they became acclimatized to tank conditions (t=11°C; S=30). The cod swimbladders were pressure adapted as the cod were caught in shallow water. Each size group of cod was transferred to the experimental set-up in turn to make separate TS measurements on each group. In order to minimize the effects of algae blooms the tank was cleaned and filled directly to a depth of 5 m with fresh Skagerrak seawater filtered through a natural sand filter just before the start of the experiments. The hydrographic conditions in the tank stayed reasonably constant during the experimental period with no thermo- or haloclines present. Only data from 3 and 10 October are included in the analyses, both being 1 day after tank refill.

Data analysis methods and data-selective criteria

For logistic reasons the echosounder was calibrated after the measurements. Acoustic raw data was replayed in the EY500 software with optimal parameter settings and the new calibration constants. The maximum allowable phase deviation was set to 4.0 and maximum allowable amplitude compensation was set to 4 dB for the echo-tracing routine in the EY500 system. The replayed data were then analysed by performing trace tracking of single fish echoes in selected layers and obtaining mean TS-values for the tracks. Tracking was performed to ensure that the mean value is calculated on the same fish in each case. The identification of tracks was performed with the EP500 software (SIMRAD, 1996b) and echo-trace data was extracted by software developed by the authors and scrutinized to include all consecutive pings actually occurring in a track. The tracks were defined as consisting of at least five consecutive pings on targets within a maximum mutual distance of 30 cm between successive target positions. Other selective criteria for data acceptance were:

- When a fish had not been within the centre of the beam field (inside a maximum total beam angle of 1.5° off axis of the acoustic beam – see below) in a track the data were rejected.
- Only measurements located within 3.5° off axis of the acoustic beam based on the calibration measurements have been included.

This means that the fish should have entered both the centre and, of course, also the periphery of the beam for data acceptance. A relatively wide margin, usually

Table 1. Mean TS, velocity (average swimming speed), depth of measurement, and number of track pings and of single fish targets as well as variation (Coeff. Var.) in backscattering cross-section and uncertainty in velocity. Also minimum and maximum TS per track, for each track is given. Comments of visually estimated tilt angle or swimming behaviour observed on the video recordings are furthermore given for each track. The tracks are subdivided by size group of juvenile cod, i.e. by date of measurement.

Date and size group	Track no.	Velocity (ms^{-1})	Uncertainty (of Vel. in %)	Target distance from transducer (m)	Pings (number)	Record duration (s)	Mean TS (dB)	CV (of bs. cross-sect.)	Min TS (dB)	Max TS (dB)	Comments and visually estimated tilt angle based on video recordings
3 Oct. 1996	1	0.099	5.3	3.15–3.21	22	2.8	−40.1	22.2	−41.2	−37.7	Swims straightly (largest fish).
Large size	3	0.050	90.1	3.06–3.06	5	0.6	−41.2	45.8	−43.4	−38.8	Swims straightly.
group cod	5	0.165	4.1	3.00–3.09	21	2.6	−44.5	40.7	−45.7	−40.9	Swims straightly to slightly downwards (medium sized fish).
	6	0.085	20.2	3.15–3.15	10	1.3	−44.9	103.9	−57.1	−39.4	Swims straightly first and then downwards (medium sized fish).
	7	0.338	11.3	3.15–3.15	6	0.8	−41.5	40.9	−46.7	−40.4	Swims straightly.
	8	0.152	5.3	3.06–3.15	17	2.1	−46.5	25.0	−49.9	−45.3	Swims tilted.
	9	0.210	18.3	2.79–2.85	6	0.8	−39.1	10.2	−39.6	−38.6	Swims straightly (largest fish).
	10	0.203	16.7	3.03–3.06	6	0.8	−44.4	94.7	−50.3	−40.2	Swims slightly tilted.
	11	0.116	9.4	3.00–3.03	13	1.6	−43.7	38.9	−49.8	−42.0	Swims slightly tilted.
	12	0.121	2.7	3.09–3.18	36	4.5	−41.4	55.7	−47.6	−37.0	Swims slightly tilted.
10 Oct. 1996	1	0.159	5.0	2.82–2.82	17	2.1	−51.1	35.7	−54.9	−48.9	(Camera not directed correctly).
Small size	2	0.176	10.1	3.00–3.00	10	1.3	−51.6	17.5	−52.5	−50.4	Swims first slightly tilted and then straightly.
group cod	3	0.416	11.3	2.91–2.91	5	0.6	−57.5	20.7	−58.7	−56.4	Swims straightly.
	4	0.102	3.0	2.85–2.91	38	4.8	−54.5	93.4	−55.6	−44.8	Swims straightly.
	5	0.407	7.0	2.91–2.97	6	0.8	−47.0	34.5	−49.2	−45.1	Dives steeply.
	6	0.102	4.3	2.91–2.94	30	3.8	−51.9	62.8	−56.6	−48.9	Swims slowly straight forwards.
	7	0.080	6.4	2.82–2.85	18	2.3	−56.6	17.1	−57.6	−55.0	Rising slightly.
	8	0.131	13.0	2.91–2.91	10	1.3	−57.0	34.6	−58.3	−54.6	Swims straightly.
	9	0.066	23.5	2.91–2.91	10	1.3	−47.1	20.3	−48.8	−45.7	Same fish diving steeply.
	10	0.138	7.6	2.85–2.91	13	1.6	−51.8	18.1	−53.5	−50.4	Swims straightly.
	11	0.126	5.5	2.94–2.97	19	2.4	−52.7	32.9	−59.1	−50.8	Swims first straightly then slightly downwards
	12	0.145	22.4	2.82–2.85	6	0.8	−58.1	17.3	−59.0	−57.1	Swims straightly.
	13	0.129	10.0	2.94–2.94	10	1.3	−58.5	13.3	−59.8	−57.5	Swims straightly.
	14	0.093	4.3	2.82–2.94	32	4.0	−53.8	37.6	−59.6	−50.2	Swims straightly.
	15	0.091	6.1	2.94–2.94	23	2.9	−57.7	38.4	−59.5	−54.8	Swims straightly.

within a distance of 20 cm, from the cage top and bottom were excluded from the analysis field in order to avoid possible interfering echoes. Multiple targets were to a large extent excluded from the analyses by the tracing routines but furthermore by examination of the concurrent video recordings. Consequently when there were more than one fish, or even the smallest risk of there being more than one, in the acoustic beam, the data were rejected.

Two software programs were developed for synchronization: one creates a file table with tape count from the video recorder vs. time in seconds. The other reads the EY500 files and creates a pingnumber vs. time table which is useful when searching for particular events during trace tracking.

Besides estimating mean TS values for the investigated fish, a principal objective of the experiment was to look at the variation in TS for a single fish in relation to its position (angle) in the acoustic beam field and its swimming speed when performing natural swimming behaviour. From the athwartships (α) and alongships (β) angles of the target in the beam field the total angle off axis (θ) in degrees from the acoustic axis can be calculated as follows:

$$\theta=\sqrt{(\alpha^2+\beta^2)} \quad (2)$$

The mean TS for each track was calculated from the mean backscattering cross-section obtained by averaging the backscattering cross-section values for each ping measured along the track. The average swimming speed (v) was obtained by:

$$\bar{V}=\bar{d} * \Delta\theta/\Delta t \quad (3)$$

where $\Delta\theta$ is the total smoothed track length in radians and $\bar{d}$ is mean depth and Δt is total track time interval. Smoothing has been performed by averaging the length of sub-tracks which are formed by using every second ping along the track.

Results

The TS measurements for each single fish track for the juvenile cod in the small (seven individuals) and large (three individuals) size groups, respectively, are shown in Table 1. Figure 3 shows in detail four examples of single fish tracks for juvenile cod in both size groups measured over a relatively large number of pings. Single ping target measurements for all the pings in selected single fish tracks are presented. In total 15 tracks for the small size group and 10 tracks for the larger size group of juvenile cod were recognized which fulfil the above given selective criteria (Table 1; Fig. 3). Although experiments were performed over some days these selective criteria, together with the use of a low ping rate to avoid reflection noise from the experimental set-up, resulted in limited data sampling and only a few usable data series to be analysed. Long stretches of data were rejected. The low number of measurements increases the variance for the mean TS due to the combined effect of tilt and directivity and weakens the TS–length-regression (Table 1). However the selected data with single ping TS measurements of one individual fish among the group of fish, within a limited size range, must, because of these selective criteria, be classified as well filtered and of relatively high quality. Longer data time series would either have prevented free swimming behaviour, e.g. the fish would have been "fixed", or the experiments should have run over months instead of days and weeks. The latter was impossible given the use of wild animals of particular size groups which had to be kept alive in natural conditions apart from the practical difficulties of preventing the stock growth outside the size range needed.

The variation in the TS measurements is calculated as the coefficient of variation (CV) of the acoustic backscattering cross-section (Table 1). The uncertainty in the target velocity is determined partly by the uncertainty in the determination of the angles of the target in both track end points, i.e. the angular deviations around the end pings. Furthermore, the uncertainty i.e. 2* angular deviations around the end pings/total track length in angular units (Table 1), is, of course, dependent on the number of pings (observations) in each track which give the track length.

For the smaller juvenile 0-group cod single ping TS values in the range of -59.8 to -44.8 dB were measured. However, in general the highest single ping TS measurements for this size class are around -46 dB (Table 1; Fig. 4). For the 15 tracks found for this cod size group the mean TS value varied from -58.5 to -47.0 dB (Table 1). For the larger juvenile cod single ping TS values from -57.1 to -37.0 dB were measured as the extremes but most values lie within the range -48 to -46 dB in the lower end to a level around -37 to -36 dB in the higher end (Table 1; Fig. 5). For the 10 tracks found for this size class the mean TS values range from -46.5 to -39.1 dB (Table 1).

In order to illustrate the variations occurring within and between the tracks Figures 4 and 5 present selected single fish tracks in which the fish can be followed both near the centre and close to the edge of the beam field. Figure 4 shows data for the group of larger cod and Figure 5 for the group of smaller fish. In general along most of the tracks the TS value varies moderately with the position of the fish in the beam field, but there are occasionally sudden or gradual large excursions of the TS value. The total variation of the TS values within each size group cannot be explained by a $20 * \log_{10}L$ relationship but may be due to either variations in tilt angle or sound incidence angle in relation to the

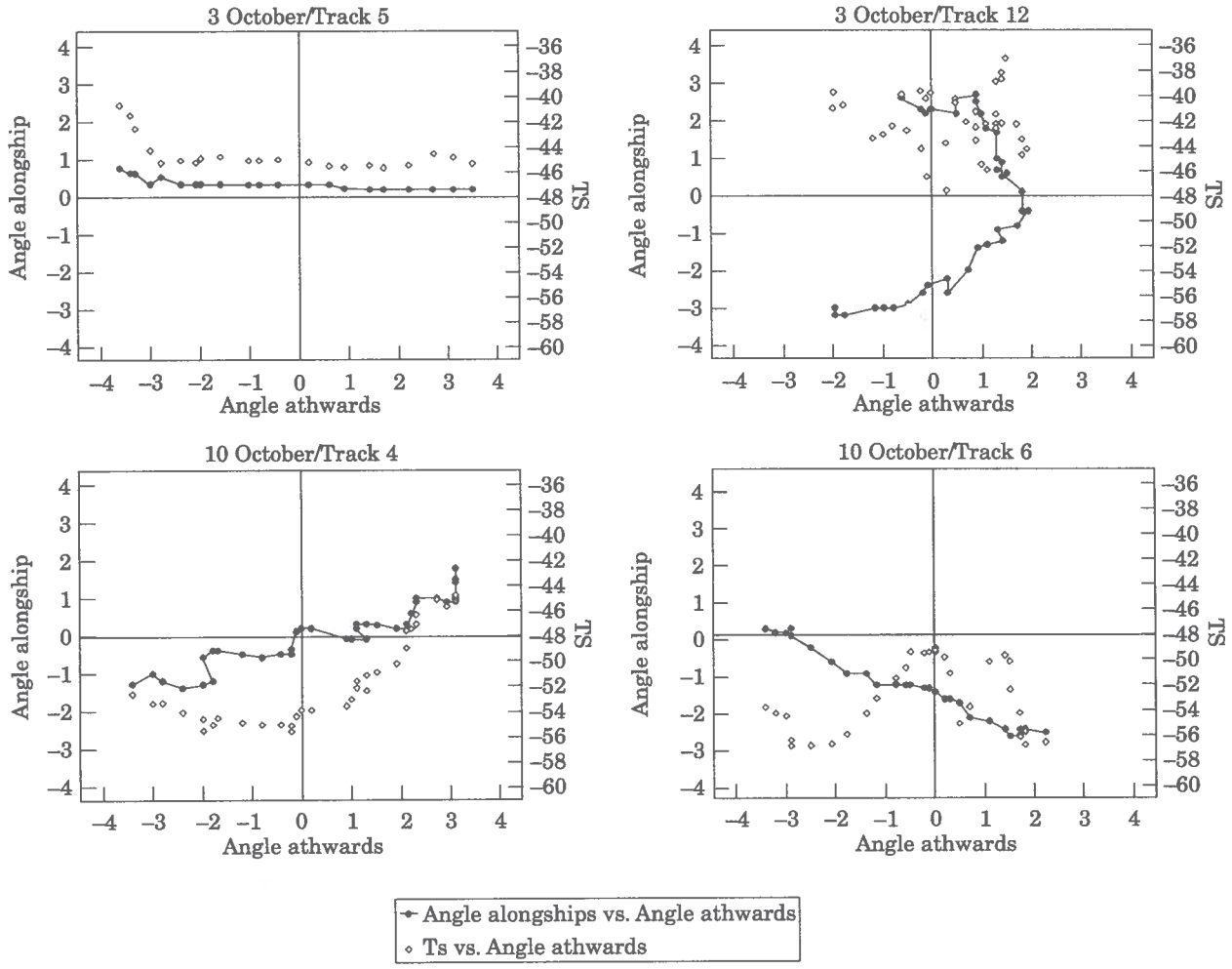

Figure 3. Plots of four examples of single fish tracks (tracks 5 and 12 from 3 October and 4 and 6 from 10 October) for juvenile cod in both the small and the large size group circulating around the centre of the beam field. These track data fulfil the criteria of at least five consecutive pings in the same track and only one fish in the beam. The plots show single ping angle alongships vs. angle athwards (in degrees) of the targets in the beam (filled circles), as well as single ping TS values vs. angle athwards (open circle) for each track.

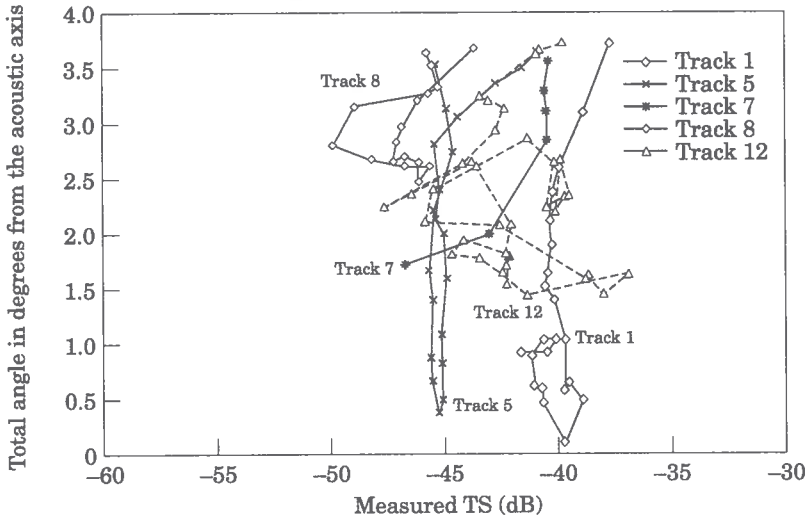

Figure 4. TS vs. total angle (degrees) for a selection of the observed single fish tracks where individuals from the large size group of juvenile cod (3 October) could be followed both in the edge and in the centre of the beam field.

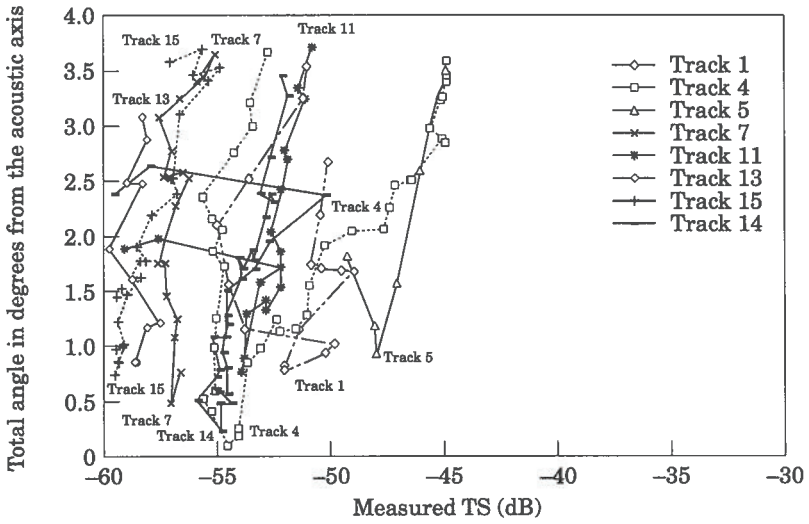

Figure 5. TS vs. total angle (degrees) for a selection of the observed single fish tracks where individuals from the small size group of juvenile cod (10 October) could be followed both in the edge and in the centre of the beam field.

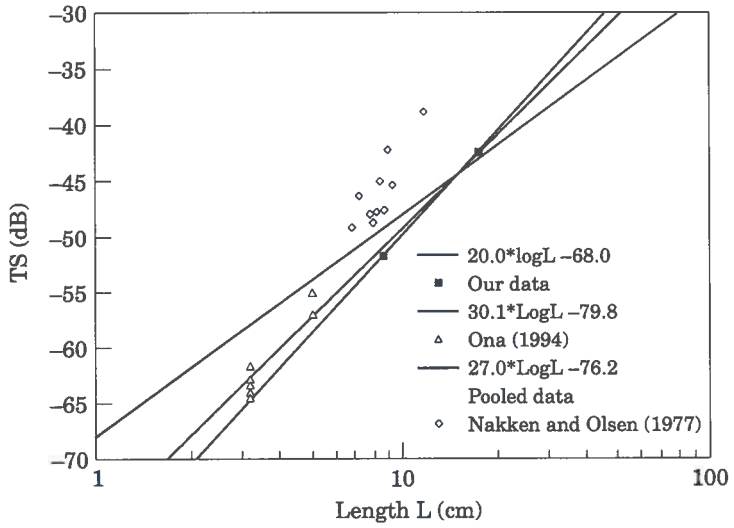

Figure 6. Plot of mean TS vs. $\log_{10}(L)$ for the two investigated groups of free swimming, juvenile cod at 120 kHz in the present study (filled squares), and the regression line (dashed) through these data. For comparison mean TS data at 120 kHz on juvenile cod measured by Ona (1994) (triangles) are shown as well as a regression line (solid) obtained by pooling our data with Ona's data. Finally data from the lower end of Nakken and Olsen (1977) plot of TS values at 120 kHz for stunned and fixed as well as anaesthetized cod are plotted (diamonds). The stippled line shows the standard TS-size relation suggested by Foote (1987).

directivity pattern of the fish, or swimbladder shape between individuals. For some tracks there might be a slight tendency towards an increase of the TS value with increasing total angle in the group of small cod. This tendency is not systematic for all tracks however and is discussed later.

When comparing the tracks for the two size groups of juvenile cod it is clear that the TS values in general are, as expected, significantly larger for the group of larger cod but the difference seems to be larger than could be explained by a $20 * \log_{10}L$ relationship. Since the number of tracks is low and it is not possible to relate the single tracks to a particular individual fish among the cod in the groups, and because not all fish within each size group necessarily are equally represented in selected tracks, the mean TS values for the two groups may be biased. However in order to illustrate the tendency Figure 6 shows the mean TS values for the two size groups under study plotted vs. the $\log_{10}$ (mean length). Mean TS is calculated as:

$$\text{mean TS} = 10 * \log_{10}(1/n\Sigma 10^{0.1 * TS_n}) \quad (4)$$

where TS_n represents the mean TS values for the separate tracks shown in Figures 4 and 5. The equation for the connecting line between the two size groups in Figure 6 is:

$$TS = 30 \log_{10}(L) - 80 \quad (5)$$

When pooling the present data with the results obtained by Ona (1994) at 120 kHz on juvenile cod the following TS relation is obtained:

$$TS = 27 \log_{10}(L) - 76 \quad (6)$$

Thus these results indicate a significantly steeper slope in the relationship between TS and fish length for juvenile cod than the traditionally assumed $20 \log_{10}L$ relationship.

Discussion

TS measurements on Atlantic cod

In reviewing TS studies of gadoids at 38 kHz Foote (1987) found that, when *in situ* measurements are not available, mean TS can approximately be estimated from:

$$TS = 20 \log_{10}L - 67.5 \quad (7)$$

where L is the mean body length (cm) of the fish (MacLennan and Simmonds, 1992). However this TS algorithm for 38 kHz is based on measurements only on larger cod.

Nakken and Olsen (1977) performed *ex situ* experiments making TS measurements on, among other species, both smaller and larger cod using 38 and 120 kHz frequencies. They found mean TS values between −47 and −40 dB (38 kHz) and −49 and −38 dB (120 kHz) for 12 small cod between 6 and 13 cm. In order to obtain these measurements though each subject fish was anaesthetized and fixed in the acoustic field (beam) by two strings. This, of course, prevented the free swimming of the fish which we have tried to ensure in the present study. Nakken and Olsen (1977) found a variability in TS from below −45 dB to more than −27 dB for the same cod (45 cm) measured at 120 kHz according to different tilt angles. As TS varies with swimbladder shape and this is regulated physiologically by the animal meeting different surrounding conditions, i.e. pressure variation related to depth and hydrography, and furthermore, the TS is dependent on the fish's natural behaviour, these TS measurements might be biased or uncertain because they are not made in a natural environment. This should be seen in light of Foote's (1980) estimate that the swimbladder is responsible for approximately 90% of the energy reflected from a fish with a swimbladder. Nakken and Olsen (1977) summarized their measurements on cod with the regression lines: $TS = 24.6 \log_{10}L - 66.6$ at 38 kHz and $TS = 24.6 \log_{10}L - 67.6$ at 120 kHz. However, the TS values measured for small, juvenile cod in these results deviate from the overall TS algorithm (regression line) for the data set covering all size groups of cod.

Ona (1994) performed *in situ* target strength measurements at 120 kHz with an ES120-7 transducer on reared juvenile cod in the size class 3–8 cm TTL (mean length 5.1 cm), and at 38 and 120 kHz on naturally living juvenile cod in the length group 2–6 cm TTL (mean length 3.1 cm) caught at sea. The measurements on the reared cod were performed within varying depth ranges, i.e. 2–7 m in the pond, and 0–45 m at sea with highest concentrations of juveniles around 15–25 m, respectively, from surface. A mean TS of −55.1 dB (range −66 to −48 dB) during evening and of −57.1 dB (range −69 to −48 dB) during night-time were estimated for the reared juvenile cod at 120 kHz. For the naturally occurring cod a mean TS of approximately −60 dB was calculated based on a selective acceptance of targets only within the mean TS range from −58.2 to −60.4 dB – the total measured TS range at 38 kHz at the locality was −78 to −47 dB. Based on this study the following working TS equation for juvenile cod at 38 kHz was calculated assuming a $20 \log_{10}L$ relationship: $TS = 20 \log_{10}L - 70$ [dB], (L = 3–10 cm). Comparative TS measurements on the naturally living juvenile cod at 38 and 120 kHz indicated a mean TS about 2–3 dB lower at 120 kHz than at 38 kHz. No TS algorithm related to length for juvenile cod at 120 kHz was given here. The problem of the swimbladder-frequency response (L/λ-relationship) as previously described might be the reason why Ona (1994) had lower values of TS at 120 kHz than expected from the standard relation for the larger cod at 38 kHz.

The single ping measurements at 120 kHz in the present study on juvenile cod within the size range 75 to 98 mm lies within the TS range from −59.8 to −44.8 dB. Furthermore, the TS measurements on larger juvenile cod within the size range −57.1 to −37 dB. Thus the variability in the present TS measurements according to fish size is actually lower than the variability in TS found in the previously performed and comparable studies on juvenile cod. The large difference obtained between 120 kHz mean TS-values for larger cod from literature and the group of smaller cod obtained in the present experiment suggests that TS for small cod decreases much faster than has been suggested by the standard $20 \log_{10}L$ relationship. This seems to agree with the tendency in Ona's (1994) data which indicates that a mean length ratio of 5.06/3.14

corresponds to a decrease of about $(-56)-(-63)=7$ dB instead of about 4 dB decrease as suggested by the standard relationship. A similar tendency is indicated by the data in Nakken and Olsen (1977), where all the data points in the lowest end lie to the left of the 120 kHz regression line. Assuming a $20 \log_{10}L$ relationship as used by Ona (1994) at 38 kHz [or a $24.6 \log_{10}L$ relation as fitted by Nakken and Olsen (1977) at 120 kHz] when measuring juvenile cod in the field on surveys then the abundance of the smaller size groups of cod will be grossly underestimated if a $30 \log_{10}L$ or a $27 \log_{10}L$ relationship is actually valid. However even though measuring at 120 kHz the problem of the swimbladder–frequency response (L/λ-relationship) cannot totally be excluded in this present study too.

The variation in TS reflects mainly variation in tilt angle of the fish, directivity of the fish itself and the behaviour of the fish. In relation to the directivity diagram of the fish the change in TS of the fish is caused by the gradual change of the sound incidence angle in relation to the location of the fish in the beam field when the fish passes (e.g. directly) through the beam (at e.g. one defined tilt angle). These factors influence the present results significantly without a doubt. A possible effect of an increase in TS of 2–3 dB as the fish moves from axis towards the border of the beam should be noted but is not found in all tracks of the smallest group of juvenile cod (Fig. 5). It is not seen, for example, in tracks 1, 13, and 14, i.e. in three out of the eight tracks for the small juvenile cod group. Attention should, of course, be paid to a possible trend here in relation to calibration but because it is not unambiguous care has to be taken in drawing conclusions from it.

The measured range of TS values for each size group of juvenile cod covers a variety of fish tilt angles and fish directivity diagrams as well as the different swimming behaviour to be expected from wild juvenile cod. The experimental cod did not show stress behaviour or significant escape behaviour during the experiments. The present data do not allow for calculation of an accurate TS relation in interpreting hydroacoustic survey results for exact biomass estimates but give a good indication of the expected range in TS for young gadoids. It should be noted that the results in this experiment were obtained in water with higher density than found in the Baltic Sea survey area. However the results give an impression of the order of magnitude of the underestimation of biomass if the standard gadoid TS algorithm is extrapolated to small size groups. The results lie within the expected range of TS values for these fish performing natural swimming behaviour and is in the same range as those presented by Ona (1994) and also in Nakken and Olsen (1977). In the present *ex situ* experiments the salinity was 30. While Baltic juvenile cod typically occur in salinities of maximum 20. This is a problem when using the present TS measurements for Baltic juvenile cod as the target strength of a fish also depends on the swimbladder morphology, which may change with seawater salinity as the fish seeks to establish neutral buoyancy. This salinity difference may cause the swimbladder volume to be slightly larger for cod in the Baltic than in the North Sea or elsewhere.

Experimental design, set-up, and *ex situ* method

The experimental design and set-up has proved to be suitable and efficient for making *ex situ* TS measurements on juvenile gadoid fish swimming freely in the acoustic beam under natural physical conditions. The experimental set-up with 3 m^3 cages may not reflect natural swimming behaviour even though the experimental fish were small juveniles for which 3 m^3 is a relatively large volume. The juvenile cod have, furthermore, been kept in groups of at least three fish in order to assure some degree of natural schooling behaviour and active swimming behaviour all over the cage. When working with a single cod in the experimental set-up pilot investigations showed that fish stayed permanently inactive in one corner of the cage or on odd occasions, swim very close to the cage bottom. The video recordings ensured that we were only measuring TS for one fish at a time in the acoustic beam. The experimental design also made it possible to calibrate easily the echosounder system in the experimental environment within the actual range of the beam where the TS measurements took place.

Suggestions for future studies

TS measurements in this experiment could only be related to single fish of known size in very few cases even though there were very few fish in each size group in the cage during each experimental series. The measured TS values are consequently only average estimates for each size group of fish with a variety of tilt angles performing nearly natural swimming behaviour. Future experiments could use all or some of the following in combination:

(1) more (two or three) video cameras in the set-up to make it possible not only to detect the presence of single fish but also to be able to estimate the exact position and tilt angle of a fish in the acoustic beam. This would require a more advanced synchronization system between video recording and acoustic data sampling than was used in these experiments;
(2) groups of fish each with a colour tag or with coding in order to visually identify and register single fish with known length and weight in the beam field from the video monitoring;

(3) smaller cages with only 1 fish in each, in order to obtain data for the exact TS range in tracks for individual fish of known size, combined with tilt angle measurements from video recordings with more than one video camera;
(4) round cages containing a known number of fish with a known length frequency distribution, to measure the mean TS for a group of fish within a given well defined size group. In this case the measurements would be based on knowing the exact number of fish in the cage and knowing the cage volume and based on the assumption that the fish on the average is randomly distributed in the cage. This could be tested by video recording.

The frequency of 120 kHz is far above the known hearing frequency range of juvenile cod and therefore avoidance behaviour related to the beam field is not expected. A study at 38 kHz (Astrup and Møhl, 1993) indicates that cod possibly do not detect high-intensity, high-frequency sound. Future studies could include investigations of avoidance reactions via video recording, for example, abrupt changes in swimming speed, swimming direction, or tilt angle, when entering the beam field. Finally future experiments could count the frequency of fish entering the beam field or estimate the density of fish in the beam when the transducer is switched on compared to when the transducer is switched off, all other conditions being equal. This would give a quantitative estimate of avoidance even when there is more than one fish in the cage.

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A method for the possible species discrimination of juvenile gadoids by broad-bandwidth backscattering spectra vs. angle of incidence

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Lundgren, B., and Nielsen, J. R. 2008. A method for the possible species discrimination of juvenile gadoids by broad-bandwidth backscattering spectra vs. angle of incidence. – ICES Journal of Marine Science, 65: 581–593.

Measurements were made of the broad-bandwidth (80–220 kHz) acoustic backscattering from free-swimming juvenile gadoids at various orientations and positions in an acoustic beam, under controlled conditions. The experimental apparatus consisted of a stereo-video camera system, a broad-bandwidth echosounder and echo-processor system, a narrowband 120 kHz split-beam echosounder, a large tank, and a fishnet cage. The net cage was centred on the acoustic beams and was virtually transparent, both acoustically and optically. Accurate three-dimensional positions and angular orientations of individual fish were estimated from stereo-images captured synchronously when broad-bandwidth echoes were received from passing fish. Fish positions were also estimated from data collected with a synchronized split-beam echosounder. Software was developed for image analysis and modelling, including calibration, alignment of acoustic and optical-reference frames, and automatic position-fitting of fish models to manually marked fix-points on fish images. The software also performs Fourier spectrum analysis and pulse-shape analysis of broad-bandwidth echoes. Therefore, several measurement series on free-swimming juvenile gadoids were evaluated. The method and data may be used to improve the acoustic identification of fish species and sizes, and thereby improve investigations of spatial prey–predator relationships, and the accuracy and efficiency of acoustic surveys.

Keywords: broad bandwidth, gadoids, species discrimination, split-beam, stereo-image analysis, target strength, tracking.

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Introduction

In fisheries research, acoustic and trawl surveys from research vessels are used to estimate the spatial distributions and biomasses of fish stocks (MacLennan and Simmonds, 2005; Kalikhman and Yudanov, 2006). The method commonly applied uses data from echosounders operating at one or more discrete frequencies (e.g. 38 and 120 kHz), and estimates the species mix and their sizes from net catches (e.g. Nielsen *et al.*, 2001; ICES, 2005a, b). The frequency dependence of acoustic backscatter from fish (see Horne, 2000; Korneliussen and Ona, 2002) could be better exploited to improve species-identification techniques. Echosounders operating over a broad frequency range (e.g. 30–200 kHz) and with a large sampling volume could provide more precise information about fish taxa or species and their size distributions in scientific investigations. Acoustic identification based on variation of the angular backscatter with frequency could, for example, ease the description of single fish prey and predator distribution patterns in the sea (Nilsson *et al.*, 2003), but may also diminish the need for frequent trawling during routine surveys (Lundgren and Nielsen, 2002).

There are good reasons to believe that species-specific, spectral characteristics for direct recognition do exist (Demer *et al.*, 1999). The fact that toothed whales use broadband backscatter when locating marine surroundings and prey (Teilman *et al.*, 2002; Beedholm *et al.*, 2006) supports the potential of the method. Multiple investigations regarding acoustic fish identification have been reported by Lebourges (1990a, b), Simmonds and Armstrong (1990), and Simmonds *et al.* (1996).

Previous investigations are of two types, either similar to ours, measuring the backscatter from a single fish, e.g. Lebourges (1990a), or directed towards measuring the backscatter from aggregations of fish, e.g. Simmonds and Armstrong (1990), Simmonds *et al.* (1996), Zakharia *et al.* (1996), and Rogers *et al.* (2004), as well as multifrequency measurements by Korneliussen and Ona (2002). Lebourges measured broad-bandwidth reflectivity of tethered trout (*Salmo trutta fario*) and sea perch (*Morone labrax*). The shape of the fish body was monitored with a two-camera system. Simmonds *et al.* (1996) made measurements of free-swimming fish aggregations, and used a single still camera to identify targets. Other researchers measured broad-bandwidth sound-scatter from *in situ* fish aggregations using modified ADCP transducers (Rogers *et al.*, 2004). In these three examples, the methods used for acoustic-target identification include spectral comparisons, and discriminant function and neural-network analyses. Their measurements, though, give only limited information on the cause of the frequency dependence of the fish spectrum and at the angle at which the greatest differences are found.

Measurements on fish aggregations need to be made with a transducer with equal beam width for all relevant frequencies, and Simmonds and Copland (1986), Simmonds *et al.* (1996), and Zakharia *et al.* (1996) designed special transducers and transceivers to obtain this information, and found spectral features in their respective frequency ranges (27–54 and 20–80 kHz) that indicated that it would be possible to distinguish between some of the species included in the investigations with a certain probability.

Our approach involved measuring *ex situ* broad-bandwidth acoustic backscattering from free-swimming individual juvenile gadoids at various orientations and positions within acoustic beams. Measurements were made on various sizes of small cod (*Gadus morhua*), whiting (*Merlangius merlangus*), and saithe (*Pollachius virens*). Characteristics of the reflected echosounder pulses are explored for possible methods of species recognition, and we suggest a methodology for discrimination, describe the experimental design, the data-collection system, and the calibration methods, as well as data analysis and modelling methodology.

Methods

The experimental set-up is an extension of the system described in Nielsen and Lundgren (1999). It consists of a stereo pair of video cameras, a broad-bandwidth (80–220 kHz) echosounder, a 120 kHz split-beam echosounder (Simrad EY500), and a large outdoor experimental tank (Figures 1 and 2). During measurements, a fish was kept centred in the acoustic beams using a net cage. Accurate three-dimensional positions and angular orientations of the fish were obtained by tracking the fish on stereo-video images, recorded when the broad-bandwidth echosounder received fish echoes (Lundgren *et al.*, 2001). The trigger signals were emitted when the echo level from a passing fish was above a selectable threshold (usually 25 mV) and corresponding roughly to the echo level from a −60 dB target in the centre of the beam at ~100 kHz within a selected distance interval (2.8–3.8 m).

General design and set-up

Tank, cage, and fish

A large outdoor tank situated at the North Sea Centre, DTU-Aqua, Hirtshals, Denmark, was used for the experiments (Figure 1). The tank, 20 m in diameter and 5 m deep, was filled with 2000 m^3 of seawater taken directly from intakes on the Skagerrak seashore. A small laboratory with an observation window (0.5 m × 1.5 m) was placed on one side of the tank.

The fish cage (Figure 1) was constructed from light nylon mesh attached to a 2 m diameter frame constructed of light plastic tube. The frame was positioned outside the main lobes of the transducers at the measurement depth. The transparency of the net was advantageous when tracking fish optically (Lundgren *et al.*, 2001). The fish were caught in the wild and acclimatized to the water temperature and cage in the measurement tank before being measured (see Data sampling below).

Instrumentation

The experimental set-up (Figures 1 and 2) consisted of three computers, the EY500, the broad-bandwidth echosounder, and a dual-camera video system. The customized broad-bandwidth sounder comprised an echo-processor (SignalData), power and signal amplifiers (Apex and Reson V1000 preamplifier, respectively), and two transducers (Reson TC2130). The sampling rates of the transmitter and receiver were both 526.3158 kHz. A pulse detector on the receiver was used to trigger the EY500 and camera systems via a signal generator (HP8111A), configured as a variable pulse-delay generator.

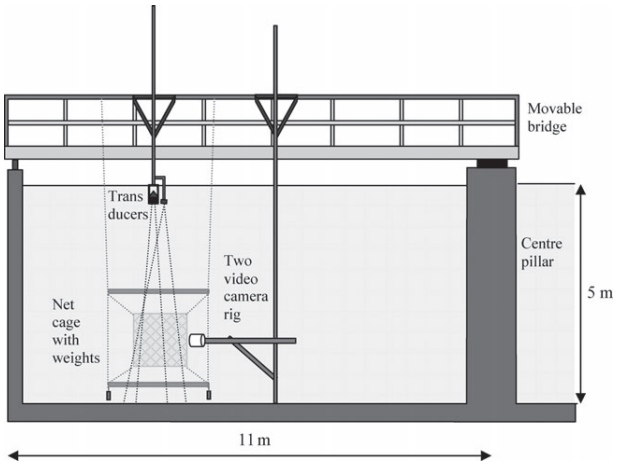

Figure 1. Section through the circular experimental tank showing its dimensions and the positions of the acoustic split-beam and broad-bandwidth transducers, fish cage, and video cameras. The cameras are placed at right angles to each other on the camera rig.

The broad-bandwidth transmitter generated constant amplitude pulses (~0.6 ms) with a linear-frequency sweep from 80 to 220 kHz. The pulses were amplified and sent to the transmitting transducer. The repetition rate was variable, but was set to ~3–4 pulses s^{-1}. The broad-bandwidth receiver digitized continuously, retaining the last 1.4 ms in a temporary buffer. When a sufficiently strong echo was received in the selected depth interval, the receiver was triggered and the buffered data were recorded. The stereo-video images were concurrently triggered. The trigger to the EY500 was delayed by 15 ms to avoid interference with the broad-bandwidth system (Figure 2). Each ping of the broad-bandwidth data contained 512 samples of the echo signal, the time and date of the trigger event, the time between the trigger event and the previous transmit event, and the sample number corresponding to the trigger event.

The image-acquisition part of the system consisted of a computer with two frame-grabber boards (Data Translation DT3152), with resolutions of 656 × 472 pixels × 8 bit, and two cameras (Sony XC55 Progressive Scan CCD) with 659 × 494 pixels, and 256 grey levels (Figure 2). The 12-mm lenses had fixed apertures. A dynamic range of about 18 dB was achieved with automatic gain control (AGC).

The two video cameras were positioned at right angles to each other, 3 m from the centre of the acoustic beams, and 3.5 m below the transducers (Figure 1). Measurements were made in the far-field of the 120 kHz transducer (see Nielsen and Lundgren, 1999). The apparatus and software are shown in Figure 2 and detailed in Lundgren *et al.* (2001).

Calibration

Optical calibration under water

The theory and procedures used in camera calibration were based on the principles given by Tsai (1986, 1987), who basically assumed a pinhole-camera model and included second-order corrections for lens aberrations. The air–window–water interface of the camera assembly (camera and case; Figure 3) acted as an

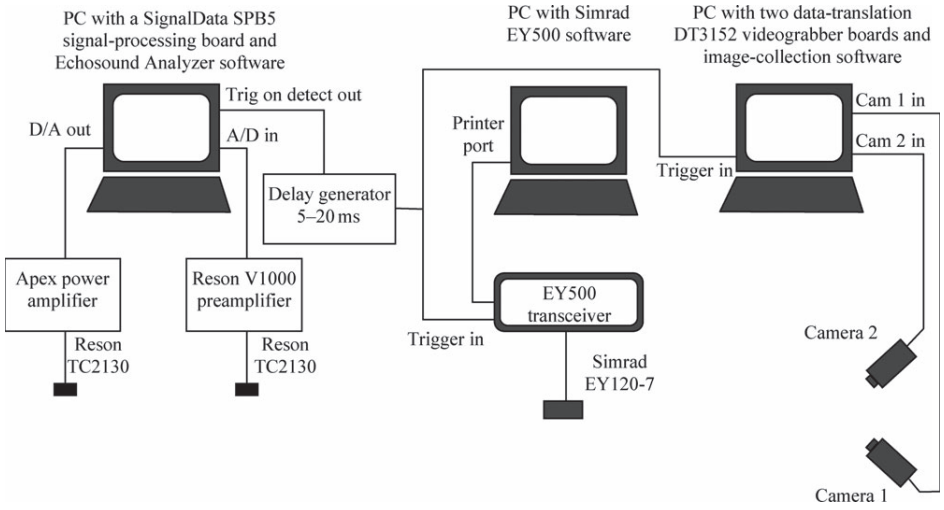

Figure 2. Schematic connection diagram for the combined acoustic and video system.

extra lens, changing the apparent opening angle, aberration and focal width of the camera assembly.

During camera calibration, the fish cage was removed and the mount for the acoustic transducers was used to support a 1 × 1 m white polyethylene plate supported by aluminium backing. On the surface of this calibration plate were 100 needles with dark, spherical heads (diameter 2.5 mm) arranged in a 10 × 10 cm matrix grid. Images were recorded with the plate at ∼45° to both cameras, and then at ∼90° to each of the two cameras (Figure 4).

The pixel positions corresponding to the needle heads in a calibration image pair were evaluated both with standard image-particle detection software (GlobalLab) and manually with the fix-point marking routine described below, with similar results. The results from the 45° exposure run were processed together with information about the camera parameters (pixel-size and pixel-aspect ratio) by Tsai's (1986, 1987) procedure for a co-planar calibration grid. The procedure is available in a C-language software package distributed on the internet (Willson, 1995). The results from the 90° runs were used to check the pixel-aspect ratio parameters. The calibration procedure estimated the apparent lens focal width, the lens distortion of the camera, and the three-dimensional position (distance and angles) of the calibration plate relative to the optical axis of the lens. From them, new constants (k_x, k_y and κ) were deduced, which provided the relationships (1) and (2) between any three-dimensional point (x_o, y_o, z_o) on the object, and the corresponding two-dimensional image point expressed in pixels (x_i, y_i):

$$x_i = k_x x_o / z_o + \kappa \tan^2(v_o) \quad (1)$$

$$y_i = k_y y_o / z_o + \kappa \tan^2(v_o) \quad (2)$$

where $\tan^2(v_o) = (x_o^2 + y_o^2)/z_o^2$.

For both the image and the object coordinates, the origin was the optical axis of the lens, and v_o was the angle between the optical axis and a particular ray through the apparent pinhole lens.

The calibration software was further developed to introduce the camera-parameter and calibration-plate data into the Tsai-calibration routines, to update the three-dimensional to two-dimensional coordinate-transformation constants, and to display the calibration data. The software also contained a model simulating a line grid corresponding to the needle-head grid on the calibration plate. This line grid could be overlaid and aligned

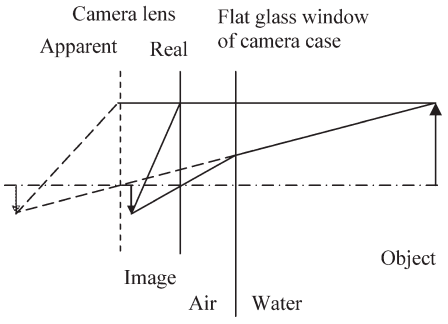

Figure 3. Geometry of the apparent change of focal width of the camera through refraction in the window–water interface of the camera case.

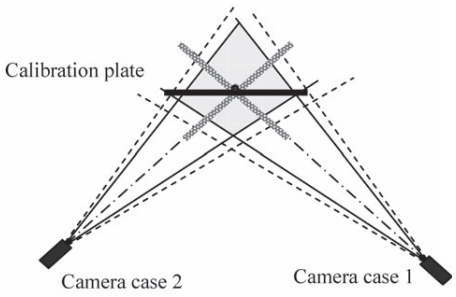

Figure 4. Positions of cameras and calibration plate during the calibration. Fine dashed and solid lines, opening angles of cameras in air and water, respectively. Bold black line, calibration plate during the main calibration. Bold grey lines, calibration plate during supplementary runs.

with the needle-head spots on the calibration-plate images, to check the calibration constants.

Calibration of acoustic systems

Shortly before the experiments, the broad-bandwidth transducers were factory-calibrated (Reson) with calibrated, reference hydrophones (Figure 5). The transmit and receive sensitivities on the acoustic axis were measured from 80 to >240 kHz in 1-kHz bands. Variations of the sensitivities with angle were measured at 100, 150, and 200 kHz in two perpendicular directions, and were represented by four-degree polynomials fitted to the measurement points (Figure 5b). Finally, sensitivity variations at other frequencies were calculated by representing the frequency variations of the second- and fourth-order coefficient by second-degree polynomials. Additionally, both the split-beam and broad-bandwidth echosounders were calibrated in the tank using a standard copper sphere of 30.5 mm diameter in the following manner:

(i) The calibration sphere was placed in the acoustic beam. Broad-bandwidth, split-beam, and video data were recorded with the sphere placed in two different positions.

(ii) The broad-bandwidth echo-pulses were selected and Fourier transformed.

(iii) The initial transducer sensitivities were applied at each frequency.

(iv) A TVG-correction referring all echo levels to 3 m distance was applied.

(v) The sphere positions obtained from the split-beam echosounder and video-tracking were aligned and used to correct the amplitude for angular-sensitivity variation of the transducers at each frequency. Aligned acoustic positions were relative to the optical centre. Like the procedure for fish described above, the software fitted a sphere model to manually marked sphere images to obtain the spatial positions.

(vi) The measured amplitude spectra were compared with theory (Figure 5a). The theoretical spectra were calculated with software (D. MacLennan, pers. comm.), using equations described in MacLennan (1981, 1982) and in MacLennan and Simmonds (2005).

(vii) Calibration corrections were calculated at frequencies of local maxima (Figure 5a), and corrections at other frequencies were estimated from linear interpolations between values at the local maxima (Figure 5a). This technique minimized potential biases attributable to measurements in the amplitude valleys having lower signal-to-noise ratios (Figure 5a). The difference in corrections between the theoretically calculated and the measured target strength were 1.00, 3.30, 2.40, −1.30, and 3.50 dB for frequencies 94, 121, 145, 170, and 196 kHz, respectively.

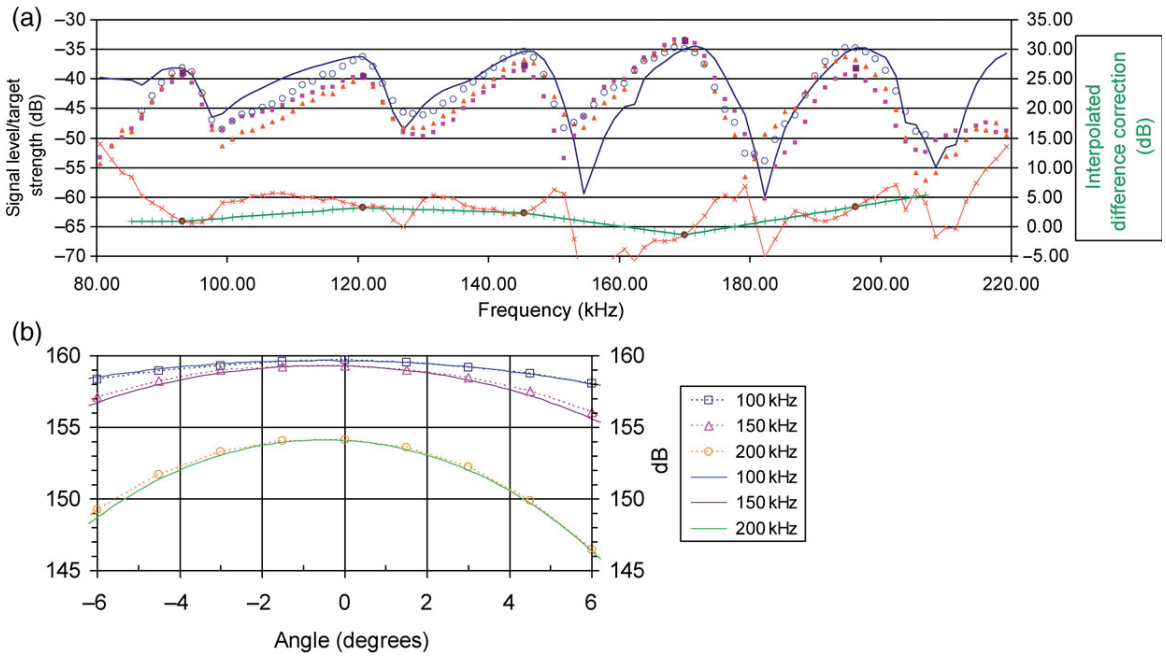

Figure 5. (a) Data from the calibration of the broadband echosounder with a 30.5 mm copper sphere. Filled triangles and small filled squares: measured sphere spectra at two different positions corrected for factory calibration, position in the beam and distance from the transducer; Large filled squares: selected peak values used for the interpolation; Solid line: running mean over 2 kHz of the theoretically calculated TS-spectrum (according to D. N. MacLennan, pers. comm.); x-x-x: difference between the average of the two measurements and the theoretical values at the same frequency; +−+−+: interpolated difference; Open circles: average measured spectrum after application of the interpolated difference correction. The corrections have been limited to the frequency range 85–208 kHz, where the SNR is acceptable. (b) Transmit lobe pattern of the TC2130 broadband transducer. One-way transmit sensitivity in dB plotted against angle at three different frequencies. Squares, triangles, and circles represent the values measured, and the solid lines represent the fourth-order polynomials fitted to the measurements.

The EY500 was calibrated using a program that logs target-strength detections of the standard sphere and estimates beam parameters and calibrated-system gains (Lobe, Simrad).

Data sampling

Measurement sessions lasted from <1 h to several hours. Most measurement sessions began with recordings of the calibration sphere at a few positions in the acoustic beam. Then, the fish were transferred one at a time from the storage tank to the net cage, and kept there for periods of half-a-day up to a maximum of ~2 d. Before this, the top of the cage was treated with soap solution, and the empty cage put in place for a while to minimize bubble accumulation. Measurements of the fish began after a few hours to avoid stress behaviour. Sessions with more than one fish in the cage were attempted, but abandoned because the fish tended to school, making it impossible or difficult to separate single-fish echoes. Recording runs were then started and allowed to continue until between 300 and 3000 image pairs with accompanying acoustic data had been collected. Between runs, the cage was carefully raised so that its topside was just above the surface, then lowered again. This removed possible accumulated bubbles.

Data processing and development of special processing and analysis software

The three dataseries were post-synchronized to a precision of ±0.1 s, utilizing the fact that pauses of variable length occurred at irregular intervals between regularly sampled data.

After synchronization, a number of groups of data corresponding to fish passes through the acoustic beams were identified and selected for further analysis within each recording run. These tracks had (i) overlapping broad-bandwidth, split-beam, and image-pair data, (ii) single-target detections from at least three consecutive pings, (iii) a maximum of one missing ping in the sequence, and (iv) a total acoustic split-beam angle detection of <3.6°. To display and visualize the data, a program was developed (ImageAnalyze; based on ImageGrab) to pair, store, and process images with the acoustic data (Figure 6). It allowed contrast enhancement of the images and inspection of the post-synchronization. Finally, to obtain the three-dimensional positions of a fish from the video images, it was necessary to identify and recognize some fix-points on the fish that were visible on both images. The program allowed manual marking, visualization, and storing of fix-points, which were later used for automatic estimation of the position and orientation of the fish.

Creation of models for individual fish

For each dataseries, a line-grid model was created to act as a visual aid in the tracking of a fish. The grid points were used to construct a line drawing of the model that could be moved around on top of each of the images in a pair, using the coordinate-conversion parameters obtained during the optical calibration described above. A number of fix-points corresponding to eyes, mouth, and fin details were enhanced to aid the operator in placing the model accurately on top of a fish image. One point, in front of the dorsal fin, was defined as the position of the fish model. A magnification factor was included to make it easy to adapt the model to a new fish of similar shape but different size. The model outline could be modified by dragging the definition points to fit a new fish in a separate window (Figure 6). The model also included an option to bend the model sideways to approximate a sub-carangiform swimming mode (see Blake, 1983; Webb, 2002). Adapting the model to swimming movements clearly improved the fit between model and images. The transformation [Equations (3)–(8) below] of the centreline of the original fish model was used (Figure 7):

$$x(0) = a_0 \times a_1 \times \sin(q_0 + q_1), \tag{3}$$

$$\mathrm{d}x(z_\mathrm{o}) = a_0 \times a(z_\mathrm{o}) \times \sin(p(z_\mathrm{o}) + q(z_\mathrm{o})), \tag{4}$$

$$x(s) = \mathrm{Scl} \times \sum_{z_\mathrm{o}=0}^{s} \mathrm{d}x(z_\mathrm{o}) \times \mathrm{d}z_\mathrm{o}, \tag{5}$$

$$z(0) = 0, \tag{6}$$

$$\mathrm{d}z(z_\mathrm{o}) = \sqrt{1 - \mathrm{d}x^2}, \tag{7}$$

$$z(s) = \mathrm{Scl} \times \sum_{z_\mathrm{o}=0}^{s} \mathrm{d}z(z_\mathrm{o}) \times \mathrm{d}z_\mathrm{o}, \tag{8}$$

where $0 < s < 100$, $\mathrm{d}z_\mathrm{o} = 1$, $p(z_\mathrm{o}) = 2\pi f_1 z_\mathrm{o}/100$, and z_o is the coordinate along the centreline of the original model. Amplitude factor and phase in Equation (4) vary along the centreline according to Equations (9)–(11) below:

$$a(z_\mathrm{o}) = a_2, q(z_\mathrm{o}) = q_0 \quad \text{for } 0 < z_\mathrm{o} \le z_1, \tag{9}$$

$$a(z_\mathrm{o}) = a_2 + a_3 \times \exp(k_1(z_\mathrm{o} - z_1)), q(z_\mathrm{o}) = q_0 \quad \text{for } z_1 < z_\mathrm{o} > z_2, \tag{10}$$

$$\begin{aligned} a(z_\mathrm{o}) &= a_2 + a_3 \times \exp(k_1(z_\mathrm{o} - z_1)) \\ &\quad + a_4 \times \exp(k_2(z_\mathrm{o} - z_2)), \\ q(z_\mathrm{o}) &= q_0 + q_2 \\ &\quad \text{for } z_2 < z_\mathrm{o} < 100. \end{aligned} \tag{11}$$

Scl is a scale factor corresponding to the actual size of the fish.

The constants $f_1 = 1$ (number of body waves per body length), $a_1 = -25$ (relative amplitude of snout movement), $q_1 = 0.3\pi$ (start phase for snout movement), $a_2 = 0.1$ (amplitude factor for basic body wave), $z_1 = 40$ (start of exponential amplitude growth as a percentage of body length), $a_2 = 0.1$ (amplitude factor for exponential growth), $k_1 = 0.1$ (growth factor for exponential growth), $z_2 = 90$ (start of the tailfin as a percentage of body length), $a_3 = 0.1$ (amplitude factor for tailfin movement), $k_1 = 0.1$ (growth factor for tailfin movement), and $q_2 = 0.2\pi$ (phase difference for tailfin movement) were predefined constants in the program, and a_0 (amplitude) and q_0 (phase) were modified interactively from the main window or the model window. The constants were initially adjusted empirically to give a reasonable visual fit between model and images in most of the image material used. The model did not include options for vertical bending, which occurred relatively infrequently.

Three-dimensional position, orientation, and bending of fish from video image pairs

Whenever model images coincided with fish images in a pair on the screen, it was adjudged that position, orientation, and bending in the model were also the position, orientation, and

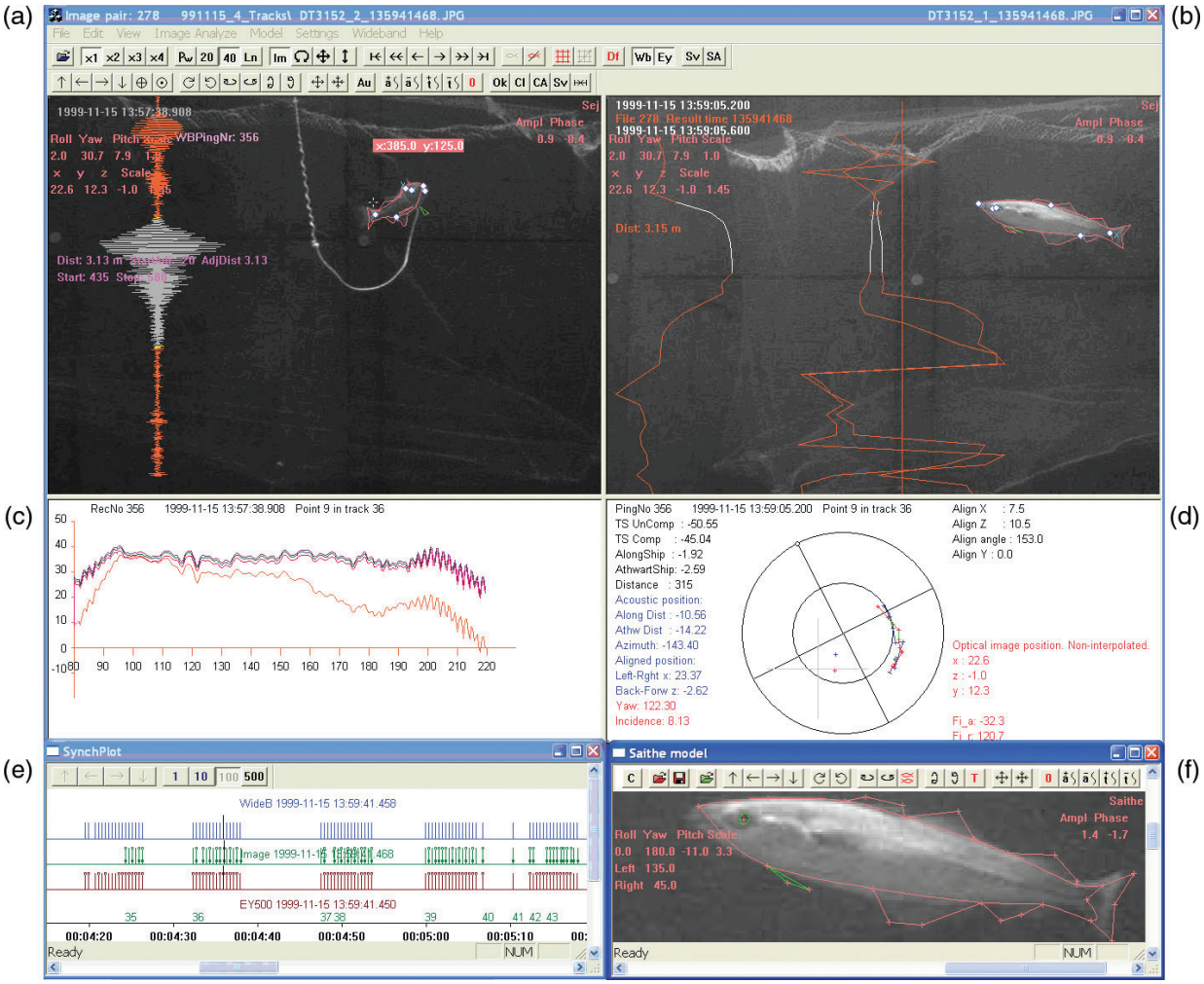

Figure 6. Main view of the data-analysis software with four permanent windows: (a) left image; (b) right image; (c) spectrum plot; (d) tracking plot; and two auxiliary windows: (e) data synchronization; (f) fish-model design. A 1.4 ms interval of the broadband echosignal can be plotted vertically in (a), starting at the top. The enhanced part is Fourier-transformed and plotted in (c) (lower red curve). The spectra corrected for transducer factory calibration, angle (target position in the beam), and depth (TVG, referred to 3 m) are also shown in (c). The split-beam amplitude and target-angle signals are plotted in (b). The enhanced part is defined by the detected depth and the pulse length. The fish split-beam position is marked with a blue circle in (d) and the optical three-dimensional position with a red circle; the corresponding position data are also shown. The crosses and lines show the 10 latest positions. The event plots in (e) show the temporal alignment of the broadband, image, and split-beam records. The crosses on the fish wire model in (f) indicate the points that can be used to modify the model after it has been aligned with a fish image using the tool bar.

bending of the fish at the time of exposure. Position (x, y, z) and angular orientation (pitch/tilt, yaw, and roll) in the reference-coordinate system defined by the stereo-image calibration, as well as the bending parameters (amplitude and phase) and magnification factor, appeared on the screen. The magnification factor is the size of the modelled fish relative to the basic model fish.

Manual and automatic fitting of the fish model to fix-points

The position, orientation, relative size (magnification), and bending of the model fish were initially adjusted interactively until the converted fish model seemed to overlap with the fish on both images correctly (manual fitting). The fitting process was aided by matching the positions of the fix-points on the fish (blue crosses) and the model (white dots).

When the fitting was satisfactory, the data describing the model fish shape (model points), the three-dimensional spatial position, orientation, relative size, and the bending parameters, together with the image-pair number and the image recording time, i.e. the trigger time obtained from the image file name, were recorded in an intermediate result file together with the target-position data (depth, athwartship, and alongship angles) from the split-beam echosounder.

To speed up the process of obtaining fish positions, an automatic, iterative fitting process with steps similar to the manual trial-and-error fitting process was designed to minimize the

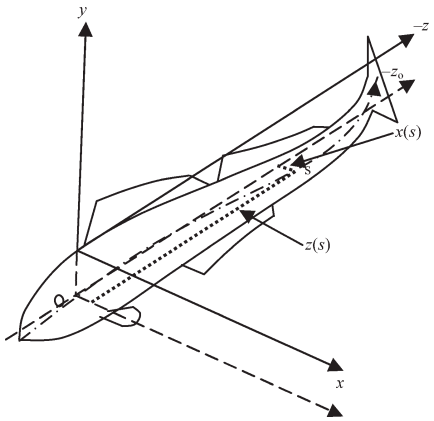

Figure 7. Coordinate system of the fish model. The position of the origin is assumed to be the position of the fish. The angle between the *z*-axis and the horizontal plane ($x-z$ plane in the camera coordinate system) is the tilt angle of the fish, and the angle between the *z*-axis and the $x-y$ plane of the camera-coordinate system is the yaw angle of the fish. The bend shape of the fish mode is described by the displacement ($x(s)$, $y(s)$) of the centreline (z_o-axis), where s is a distance along the centreline.

mean distance between the manually entered fix-points and the model fix-points on the images. Automatic fitting included the x, y, and z coordinates and the pitch and yaw angles, but not the roll angle or the bending parameters. However, the last two parameters could be interactively updated, whereas the automatic fitting of the other parameters was active.

As the cameras were approximately at right angles and equidistant from the fish, the iterative process was initialized by setting the model pitch-and-yaw angles equal to estimated fish pitch-and-yaw angles calculated by directly using the pixel distances between the available fix-point pairs on the fish images. On the first image, the model-fish position was initialized to (0, 0, 0), otherwise the position obtained in the last iteration process was used. The initial pixel positions of the model fix-points on the images were calculated using Equations (1) and (2) (see the Optical calibration section). Then, the model position was incremented a small amount beginning with the y-coordinate (up or down), and new positions for the model fix-points on the images were calculated. A first estimate of the actual vertical position of the fish was then calculated by assuming that the ratio between the two distances (fish position to initial fish-model position, and incremented fish model position to initial fish model position) in the camera coordinate system was the same as the ratio between the corresponding distances in the image-pixel coordinates, i.e.:

$$(y_f - y_{mo})/(y_{md} - y_{mo}) = \mathrm{AvDist}(\mathrm{fxp_{if}}, \mathrm{fxp_{imo}})/\mathrm{AvDist}(\mathrm{fxp_{imd}}, \mathrm{fxp_{imo}}), \quad (12)$$

$$\text{or } y_f = y_{mo} + (y_{md} - y_{mo}) \times \mathrm{AvDist}(\mathrm{fxp_{if}}, \mathrm{fxp_{imo}})/\mathrm{AvDist}(\mathrm{fxp_{imd}}, \mathrm{fxp_{imo}}), \quad (13)$$

where y_f is the estimate of the y-coordinate of the fish, y_{mo} the y-coordinate for the original model position, and y_{md} is the incremented position. The function AvDist($\mathrm{fxp_1}$, $\mathrm{fxp_2}$) calculated a weighted mean pixel distance between two image fix-point sets. The name $\mathrm{fxp_{imo}}$ represents the set of model fix-points in the images with the model in the initial position, $\mathrm{fxp_{imd}}$ with the model in the incremented position, and $\mathrm{fxp_{if}}$ the set of fix-points on the fish images. The magnitude and sign of the weights depended on which variable (y, x, z, pitch, or yaw) was incremented. The model position was changed to the newly estimated position and the iteration loop repeated until AvDist($\mathrm{fxp_{if}}$, $\mathrm{fxp_{imo}}$) was <1 (pixel). A similar iteration loop was done for each of the other variables: x, z, pitch, and yaw, in that order. The whole set of iteration loops were repeated until the <1-pixel condition was fulfilled for all variables simultaneously. Finally, for each image pair, the automatic fitting process was checked manually.

Fish tracking and alignment of optical and acoustic tracks

The actual position of the fish in the horizontal ($x-z$) plane as defined by the model position, and the split-beam data were plotted in the tracking window (Figure 6d). The position data (in the intermediate file) closest in time to the then displayed image pair were plotted as track lines. The program also included an option to move the origin and rotation of the acoustic-reference coordinate system interactively, to align the optically and acoustically measured tracks in the best possible way (Figure 6e). The alignment parameters were stored in the intermediate data file mentioned above, whenever it was updated.

Display of the echo-amplitude of the acoustic broad-bandwidth data

The interval of ~1.4 ms of broad-bandwidth pulse data recorded was displayed as a plot of the echo-amplitude against time along a vertical axis (Figure 6). From start to end of the fish-echo pulse, the pulse was highlighted by a different plot colour. The start was defined by the trig-sample number and a pulse-start adjustment parameter, and the fish-echo-pulse length was assumed to be equal to the transmit-pulse length (~0.6 ms). The depth calculated from the delay time between start of the transmit pulse and start of the echo pulse (sound speed 1478 m s^{-1} at a salinity of 32 psu and a temperature of 8°C) was also displayed on the screen. The pulse-start adjustment parameter, which compensates for the delay between the actual pulse-start time and the trig time, was stored in the intermediate output file when next it was updated. The software allowed for interactive modification of both pulse-start and -length parameters.

Fourier spectrum analysis of the broad-bandwidth echo pulse

The actual fish pulse data as defined by the pulse-start and -length parameters (default 300 samples plus some margin) were extracted to a 1024-point buffer, and the rest of the buffer was zeroed. The first five and the last five samples were multiplied with a Gaussian-shaped function to diminish possible ringing caused by sharp pulse edges. The data in the buffer were then converted to a spectrum by a 1024-point Fourier transformation. The real and imaginary components of the spectrum were combined into a power spectrum.

Display of uncorrected and corrected Fourier spectra

The part of the spectrum corresponding to frequencies between 80 and 220 kHz was plotted as power in dB against frequency in kHz (Figure 6c). A curve representing the power spectrum compensated by the transducer-calibration factors was also displayed. Using the lobe-shaped pattern of the broad-bandwidth transducers, an amplitude correction was obtained by assuming that the

actual target position (angular distance from beam axis) in the broad-bandwidth beam was the same as obtained by the target tracking with the split-beam echosounder or with the optical tracking after alignment. Small errors in the target angle will not affect the correction for the broad-bandwidth hydrophones significantly, because the main lobe is much wider and flatter for all frequencies than the split-beam main lobe. The lobe pattern was derived by interpolation as described above. The curve of the compensated power spectrum was also displayed.

Output data

Each measurement series was stored in a hard-disk file containing a record for each image pair with its number and name (time), the species name, a track number, and the image-pair number within the track. For each image pair with an accepted model fit, i.e. where fish position was well-defined by fix-points directly or could be determined by interpolation between the two adjacent image pairs, the position, angle, and bending data of the fish as obtained by model fitting were also stored. If an acoustic position was available from the split-beam echosounder, it was stored together with ping number, time, and measured target strength (compensated and uncompensated). Accordingly, broad-bandwidth data were stored as record (ping) number, ping date and time, and pulse data. Finally, auxiliary data, such as the alignment parameters between the optical and acoustic positions, the adjustment parameter to align measured split-beam, the broad-bandwidth depths, and a data-status byte, were also stored. The pulse data consisted of two parts. The first was 19 samples of the pulse amplitude as a function of time; each sampled the mean square amplitude of 16 samples of original data, i.e. 304 samples starting at the adjusted trigger point. The second was 19 samples of the Fourier spectrum of the pulse; each sampled the root mean square of 15 samples of the original power spectrum corresponding to frequencies of ~80–220 kHz. The data-status byte indicated which data types were available for each image pair.

Apparent acoustic tilt angle of a fish

The calibration plate used for optical calibration as described earlier was aligned with its vertical axis parallel to the axis of the acoustic beam. The acoustic tilt angle of a fish, defined as the angle between an acoustic ray from the centre of the transducer to the "fish" coordinate origin and the y-axis of the fish (see Figure 7), is equal to the tilt angle when the fish is positioned on the beam axis. For most other positions of the fish, this angle will differ from the tilt angle. An approximate apparent acoustic tilt angle was calculated as the angle between the fish y-axis and the projection of the acoustic ray on the vertical (y–z) plane of the fish according to Equation (14) (see Discussion for motivation):

$$\begin{aligned}\cos(90 - \mathrm{tt_a}) &= \cos(\mathrm{yw}) \times \cos(\mathrm{tt}) \times \sin(\nu_{\mathrm{athw}}) - \sin(\mathrm{yw}) \times \\ &\quad \cos(\mathrm{tt}) \times \sin(\nu_{\mathrm{along}}) + \sin(\mathrm{tt}) \times \cos(\nu_{\mathrm{tot}})\nu_{\mathrm{tot}} \\ &= \mathrm{sqrt}(\nu_{\mathrm{athw}}^2 + \nu_{\mathrm{along}}^2), \end{aligned} \quad (14)$$

where $\mathrm{tt_a}$ is the apparent tilt angle, tt the tilt angle, yw the yaw angle, and ν_{athw} and ν_{along} are the two angles defining the angular distance of the target from the acoustic beam.

Results

The results are based on five measurement series, as summarized in Table 1. Figure 8 shows the power-spectrum data of the series as the relative variations in dB plotted against the estimated acoustic tilt angle of the fish. This incidence angle depends on the position of the fish relative to the beam axis and the swimming direction (yaw) of the fish, as defined above.

Table 1. Summary of data obtained from the experiments.

Fish species	Fish length (mm)	Fish weight (g)	Number of accepted pings/ image pairs	Tilt range(°)
Whiting	140	23	387	−13–+34
Whiting	149	27	93	−8–+13(+35)
Saithe	199	80	675	−9–+32
Cod	125	14	300	(−10)−3–+36(+45)
Cod	160	37	146	−17–+11

The number of unaccepted echoes using the described selection criteria was several thousands, especially for saithe. The tilt indicates the range of high-density data, and the numbers in parenthesis indicate range extensions with lower density data.

Patterns of the backscattering vs. tilt angle vary with frequency for all species and size groups (Figure 8). These directivity patterns resemble some of the patterns obtained in the modelling work presented by Clay and Horne (1994) and Jech and Horne (2001). Those authors used the Kirchhoff–Ray mode (KRM) theory and measurements of anatomical structure obtained from X-ray photographs to construct models that explain theoretically the physiological and anatomical features in fish directivity patterns.

Here, a simple physical model using length alone was fitted to the data to identify species dependence in frequency-dependent directivities:

$$\begin{aligned}\mathrm{A_{model}} &= \log_{10}((\sin(C_1 f \sin(\mathrm{tt_a}))/(C_1 f \sin(\mathrm{tt_a})))^2 \\ &\quad + K_1(\sin(C_1 f \sin(\mathrm{tt_a})/4)/(C_1 f \sin(\mathrm{tt_a})/4))^2 + K_2) + \\ &\quad K_3(f), \end{aligned} \quad (15)$$

where $\mathrm{tt_a}$ is the incidence angle according to Equation (14), and f the frequency. The values of the parameters C_1, K_1, and K_2 were selected manually to give the best possible fit visually to the log-amplitude data in Figure 8a–e, so giving one set of parameters for each species and size. In each of these cases, the parameter $K_3(f)$ was determined for each of the 18 frequencies in such a way that the mean values of the log-amplitude data and A_{model} over a selected angle interval were equal. The constant C_1 is proportional to the selected characteristic length in the model.

As both K_1 and K_2 are much smaller than 1, the square of the Sinc function appears to explain most of the backscattering directivity patterns (see Denbigh, 1998). Despite the quasi-independent parameters, similarly shaped curves resulted. Consequently, these data could not be used for unambiguous discrimination of species or size. Moreover, visual scrutiny of the plots of amplitude against tilt angle (Figure 8) also failed to identify unambiguous distinctive patterns. For cod, however, there seems to be a distinct pattern in the backscattering for angles of incidence from 20° to 40°. For cod of both size groups, there is only one main lobe (−10° to −5°) and smooth side lobes (20–40°), compared with the other species. Whiting also have a strong main lobe, but have distinct side lobes, especially the first-order side lobes. There were too few observations to describe the main lobes for

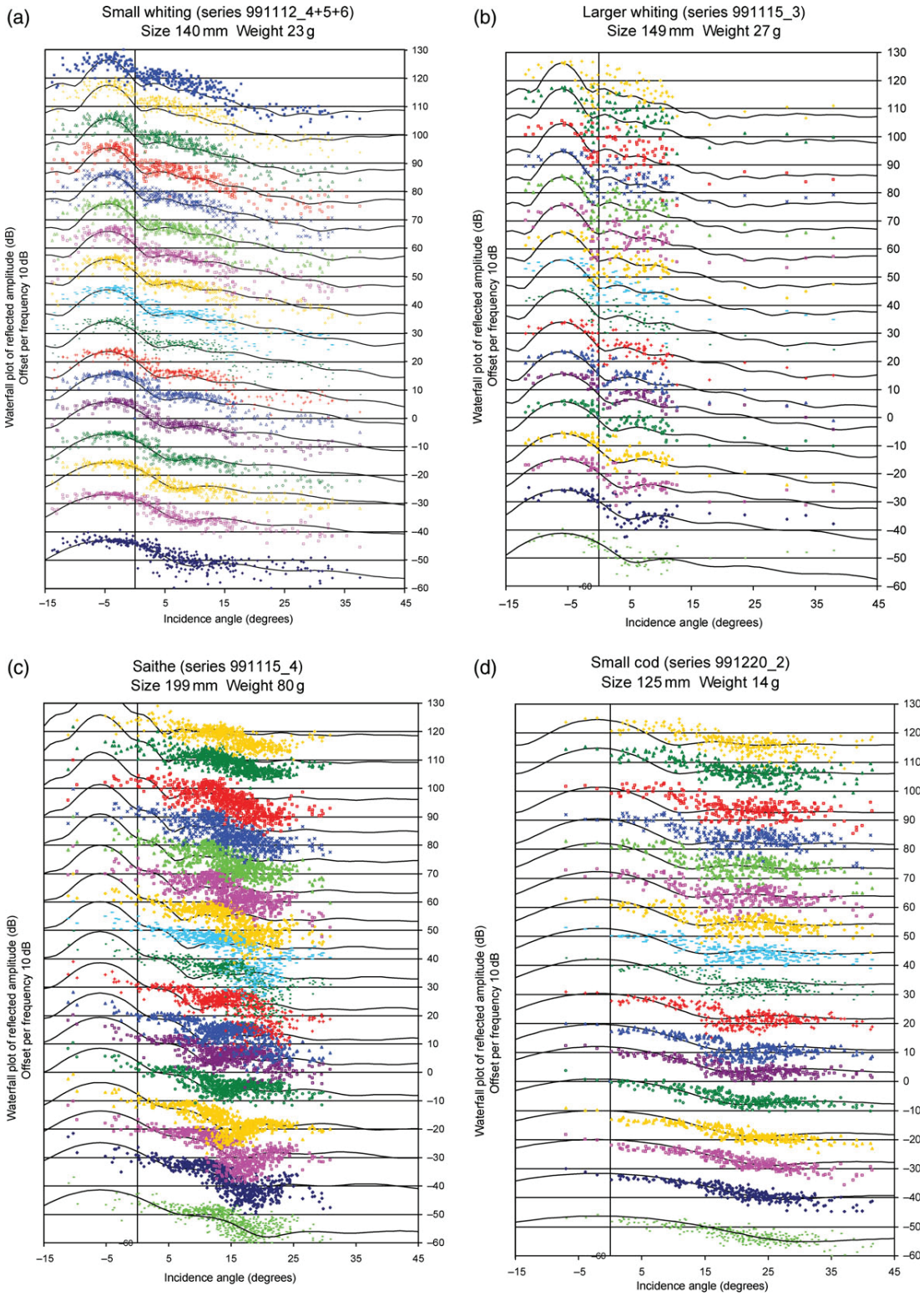

Figure 8. Backscatter power-spectrum data as a function of pitch and frequency from the five measurement series on single, free-swimming, juvenile gadoids. (a) Small whiting, (b) larger whiting, (c) saithe, (d) small cod, and (e) larger cod. The figure shows the collection of instantaneous spectra of the echopulses received from the fish. Each spectrum consists of 17 points vertically at the corresponding incidence angle, and each point represents the energy averaged over a frequency interval of 7.8 kHz. The equidistant centre frequencies range from 83.3 to 208.3 kHz. For clarity, the plots of the different frequencies have been separated by 10 dB, with the lowest frequency at the bottom. Incidence angle is the pitch angle corrected for fish position and yaw (swimming direction). The solid lines represent the functions fitted to the data points (see text).

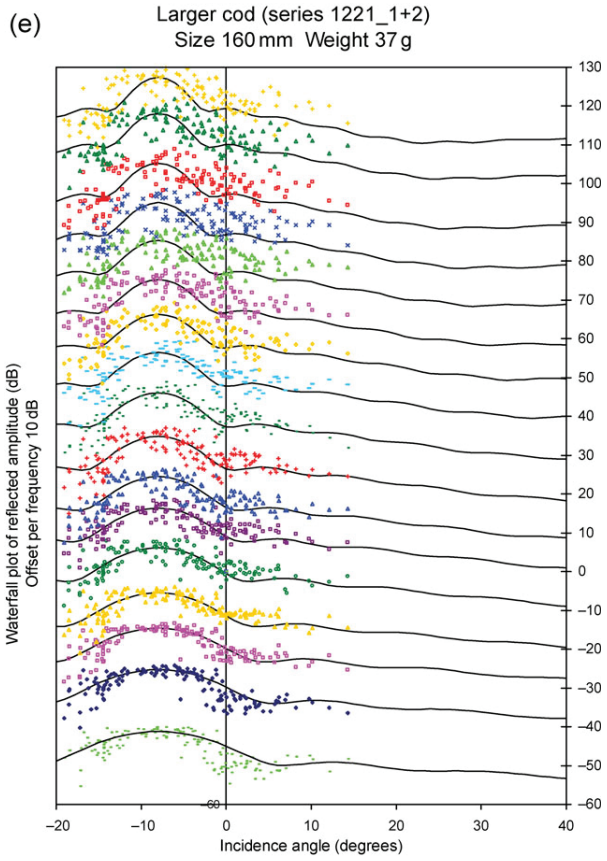

Figure 8. Continued

saithe. However, distinct patterns do appear in the side lobes of saithe. In contrast to the other species, saithe have distinct second-order side lobes, with distinct nulls between the first- and second-order lobes.

Statistical discriminant function analyses (DFA) based on a principal component analysis (PCA) was also looked at in terms of its potential to distinguish species- and size-specific patterns in the backscattering. The PCA and DFA analyses were carried out with the R-functions princomp (PCA) and lda (linear discrimination) in the R-2.3.1 package (Ithaka and Gentleman, 1996; Venables and Ripley, 1996). Variables included in the analyses were fish species and length/weight (individual fish), tested with respect to dependence of fish position and orientation, i.e. acoustic incidence, pitch and yaw, for acoustic broad-bandwidth amplitudes at different frequency intervals with midpoints of 83, 91, 99, 107, 115, 122, 130, 138, 146, 153, 161, 169, 177, 185, 192, 200, 208, and 216 kHz within the measured broad-bandwidth frequency range of 80–220 kHz.

The PCA analyses were performed for each fish to compare principal components between individuals. They revealed that when yaw is included, the first principal component was solely dependent on this variable for all fish. This means that the other variables were independent of yaw. Accordingly, yaw was removed as a describing variable. As acoustic incidence angle is a direct function of yaw and pitch, pitch was also removed from the analysis, so only the acoustic incidence angle was retained. Therefore, PCAs were used to explore relationships between acoustic incidence and acoustic reflection (amplitudes) for each fish. The second round of PCAs revealed that the first principal component for all individual fish included all descriptive variables, with approximately equal weight. The first principal component was dominant for all fish, and the second included in general half of all the variables, though no common patterns could be found.

The quadratic DFA demands underlying normally distributed amplitudes (Venables and Ripley, 1996), but a Shapiro–Wilks test showed the distribution to be significantly different from normal. Accordingly, a series of linear DFAs was tested to identify the best model to describe the variability in data. The general linear DFA model used with different modifications was of the form

$$\begin{aligned} \mathrm{ldl} = \mathrm{lda}(\mathrm{species} \sim \mathrm{length} \times \mathrm{AcuIncid} \times \mathrm{AmpF83} \times \mathrm{AmpF91} \times \\ \mathrm{AmpF99} + \mathrm{AmpF107} + \mathrm{AmpF115} + \mathrm{AmpF122} + \mathrm{AmpF130} + \\ \mathrm{AmpF138} + \mathrm{AmpF146} + \mathrm{AmpF153} + \mathrm{AmpF161} + \\ \mathrm{AmpF169} + \mathrm{AmpF177} + \mathrm{AmpF185} + \mathrm{AmpF192} + \\ \mathrm{AmpF200} + \mathrm{AmpF208}, \end{aligned} \quad (16)$$

where ldl is the linear discrimination line, lda the linear discriminant analysis, AcuIncid the acoustic incidence, and Amp the amplitude for a distinct frequency, *F*.

Modifications of the model (Models 1–5) are summarized in Table 2. Some DFAs included fish length (Models 4–5) and some did not (Models 1–3). All DFAs included acoustic incidence angle and all amplitude variables. All models were basically

Table 2. Results from statistical linear DFA performed in R.

Model	Length variable	Interaction effects	Correlation
Model 1	Not included	None	0.69
Model 2	Not included	Acoustic Incidence*Amp83*Amp91*Amp99*Amp107	0.82
Model 3	Not included	Acoustic Incidence*Amp208; Amp177*Amp185*Amp192*Amp200	0.75
Model 4	Included	None	0.86
Model 5	Included	Length*Acoustic Incidence*Amp83*Amp91*Amp99	0.92

Ampxx, mean square spectrum amplitude in dB averaged over 7.8 kHz; xx, the frequency at the midpoint in kHz (see also the plots in Figure 8).

additive models, but included different first-order interactions between specific amplitude variables and acoustic incidence. The different interactions in the models are shown in Table 2. To validate the results obtained by the linear DFA, a cross-validation was performed comparing the different models. Here, half the observations were arbitrarily sampled and used to establish a prediction surface from linear discrimination. This surface was used to test how well one can predict in the other 50% of the data. This experiment is repeated a number of times through simulation, to establish the probability of success of correct classification. Figure 9 shows the results of this, along with the probability (or proportion) of correct classification with 95% confidence limits by the tested DFA model.

The results (Table 2, Figure 9) indicated that DFAs can discriminate between different species. The correlation ranged from 0.69 for the pure additive model without the length variable included (Model 1) to 0.92 for the model including length and four interaction effects between the amplitude variables and the acoustic incidence (Model 5). The apparent power of this analysis may be an artefact of discriminating a few species groups using many variables extracted from many observations of a few fish. Consequently, the DFA method must be assessed further and tested on more fish, and *in situ*. However, the cross-validation test indicates some robustness in the statistical results.

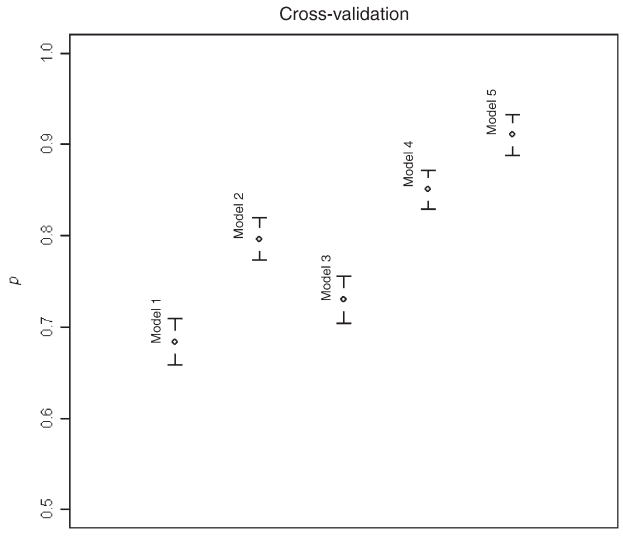

Figure 9. Results of the cross-validation giving 95% confidence limits for the probability (p) of correct classification (fish recognition) based on linear DFA in relation to the different models.

Discussion

In this exercise, we studied the spectral characteristics of the backscattering from single free-swimming fish with the purpose of extracting possible useful features for direct recognition of species. The beam angles of the measurement transducers were frequency-dependent. To measure the frequency-dependence of the backscattering directivity pattern, it was necessary to monitor continuously the positions of the fish in the beam. This was done both acoustically and optically. The results strongly indicate narrow main lobes, suggesting that the pitch or tilt angle of the fish is the dominant determinant of variations in target strength. This is even true for relatively small, single fish. The frequency response is relatively flat for small pitch angles, but variations increase with increasing pitch angle. These findings agree with the modelling results of Clay and Horne (1994) and Jech and Horne (2001).

The formulae above are based on the assumption that for a relatively limited target-angle range of $\pm 3.5^{\circ}$, it is sufficient only to consider the acoustic tilt angle and to ignore roll. The shape of the scattering pattern from fish (swimbladder) is relatively circularly symmetrical around the roll axis, as shown clearly by the modelling results of Jech and Horne (2001) and Towler *et al.* (2003).

The cage appeared to work well during the measurements. There were some distinct, but relatively weak echoes, somewhat variable in amplitude, corresponding to the top and bottom of the cage, but no noticeable interference in the range of distances at which the fish echoes were accepted.

The inherent advantages of the standard-target acoustic calibration method are that it easily gives corrections of the initial calibration constants, takes both the electrical and acoustic properties of the signal path from transmitter to receiver, and is usable for ship-mounted transducers. Moreover, the whole frequency range is measured simultaneously, and only a few sphere positions are needed for the daily routine calibrations. However, owing to the valleys in the sphere spectrum (Figure 5), the disadvantage of the method is that the signal-to-noise ratio was low at some frequencies. It was, therefore, necessary with interpolation to obtain corrections for all frequencies. Acoustic calibration should be improved by using several calibration spheres with different diameters to get more evenly distributed high-level calibration data, even though this would increase the required calibration time.

The acoustic-calibration procedure included the assumption that one can interpolate the correction constants linearly between the values at the measured frequencies (Figure 5). The difference lines shown in Figure 5 indicate that this assumption is reasonable, and that uncertainty is only in the relatively low-amplitude values.

Two methods of obtaining the position of the fish based on the fix-point positions in the three-dimensional images were considered at the start of the project. In the direct method, the parameters for lines in the object space corresponding to light rays passing through the fix-points in each image and the aperture centre point of the corresponding camera have to be calculated. In theory, the intersection points of these lines in the object space will give the positions of the object fix-points. However, because the image fix-points were marked on a small target with low contrast, there were errors in the estimates that were sometimes large and clearly varied from point to point in the same fish image. This would have made it very difficult to make a proper estimate of the actual position of the fish, particularly in the direction in and out of the picture. Therefore, in the indirect method used here, a set of points outlining a fish line-grid model with fix-points was defined in the object space, and the positions of the corresponding sets of model points in the images were then calculated. The position and angular attitude of the model were then changed by manual or automatic iteration until a suitable fit of the fish and model images had been obtained. This has several advantages over the direct method. As contrast in the images was generally low, the small errors in placing the image fix-points would have caused the calculated ray lines not to intersect, making it difficult to calculate probable positions of the object fix-points. With the indirect method, the relative positions of the calculated object fix-points were always the same. Therefore, an averaging effect with regard to the position of the centre point of the model could be obtained. Also image-position data for fix-points, which were visible in only one of the images in a pair, could be used, and points or contours other than those defined as fix-points could be used visually to aid the position fitting. Finally, obviously erroneous automatic fits could relatively easily be spotted and corrected manually.

More data should be obtained from individual and aggregated fish of more species to obtain the parameters required for accurate species recognition. Future laboratory experiments should also include a broader frequency range (e.g. 20–400 kHz). All data collections should be synchronized centrally and immediately, avoiding uncertainty in the synchronization process. Multiple calibration spheres with different diameters should be used to obtain measurements with high SNR levels across the full bandwidth. Low-light cameras with high pixel densities and colours should be used to improve image contrasts and optical tracking of fish. The dynamic range of the broad-bandwidth system should also be increased.

The corrections for incidence angles did not reduce the variations in echo-amplitude vs. tilt angle, as expected. Therefore, more work may be needed to model the acoustic tilt angle and the influence of swimming movements on the backscatter. The shapes of the backscattering-directivity pattern may be used to identify fish species and their sizes. This could be measured *in situ* from multiple observations as a fish swims through the broad-bandwidth beam, or more synoptically using a multibeam, broad-bandwidth transducer. Because broad-bandwidth systems have shorter detection ranges than most narrow-bandwidth echosounders, they may need to be deployed on towed bodies or on autonomous underwater vehicles to allow them to get closer to the fish.

To conclude, synchronized, broad-bandwidth, acoustic backscattering and accurate three-dimensional positions and angular orientations of individual free-swimming fish have been made under controlled conditions. This was done through specially developed experimental design and data-analysis software. The characteristics of the broad-bandwidth, backscattering-directivity patterns were investigated for possible acoustic fish-species recognition methodology. The results, while inconclusive, suggest that it is possible to discriminate acoustically between some free-swimming juvenile gadoids, at least under experimentally controlled conditions.

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Chapter 4

Analysis of trawl survey catch rates to estimate total and natural mortality, sexual maturity and growth of Norway pout in the North Sea associated to density dependence

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Do Norway pout (*Trisopterus esmarkii*) die from spawning stress? Mortality of Norway pout in relation to growth, sexual maturity, and density in the North Sea, Skagerrak, and Kattegat

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The mortality patterns of Norway pout (NP) are not well understood. It has been suggested that NP undergo heavy spawning mortality, and this paper summarizes and provides new evidence in support of this hypothesis. The very low–absent fishing activity in recent years provides a unique opportunity to analyse the natural life-history traits of cohorts in the NP stock in the North Sea. Based on the ICES trawl survey abundance indices, cohort mortality is found to significantly increase with age. We argue that this cannot be explained by selectiveness in the fishery, potential size-specific migrations out of the area, higher predation pressure on older individuals, or differences in survey catchability by NP age from before to after spawning and that it is higher in the main spawning areas than outside. We found that natural mortality (M) is significantly correlated with sexual maturity, sex, growth, and intraspecific stock density. All of this is consistent with a greater mortality occurring mainly from the first to the second quarter of the year, i.e. spawning mortality, which is discussed as being a major direct and indirect cause of stock mortality.

Keywords: cohort analysis, density-dependence, growth, maturity, natural and fishing mortality, North Sea, Norway pout, population dynamics, spawning, spawning stress and mortality, *Trisopterus esmarkii*.

Introduction

The North Sea–Skagerrak–Kattegat Norway pout (NP; *Trisopterus esmarkii*) stock is an important food source for commercially important fish species, such as cod (*Gadus morhua*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), and whiting (*Merlangius merlangus*). Therefore, this small, short-lived species is an important prey organism in the North Sea ecosystem (Sparholt *et al.*, 2002a; ICES, 2008; Rindorf *et al.*, 2010). In addition, the NP stock is usually a direct target of a significant small-meshed fishery for reduction (industrial) purposes (ICES, 2007a, b, c, 2010).

The time-series of the NP stock mortality shows substantial differences between natural mortality by age as estimated by Sparholt *et al.* (2002a), the MSVPA (multispecies virtual population analysis) model, and the SURBA (survey-based assessment) model (ICES, 2004, 2006, 2008; Supplementary material). Despite these differences, constant values of natural mortality of $M = 0.4$ per quarter for all ages are still used in the ICES single-stock analytical assessment (ICES, 2010).

Although mortality by predation of the NP stock decreases or remains somewhat constant as fish grow older, based on documentation from existing stomach sampling programmes and MSVPA analyses (Sparholt, 1994; ICES, 2006, 2008; Rindorf *et al.*, 2010), total natural mortality increases with age (Sparholt *et al.*, 2002a, b). Total mortality is also substantially higher than the fishing mortality documented through the ICES single-stock assessments (Sparholt *et al.*, 2002a; ICES 2007a, b, c, 2008, 2010). As a result, total mortality (Z) cannot be exclusively explained by fishing activities and direct predation mortality;

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there is another important source of natural mortality. The highest total mortality rates have been observed between the first (Q1) and second (Q2) quarters of the year, which correspond to the spawning season (Sparholt *et al.*, 2002b; Lambert *et al.*, 2009).

Residual mortality, i.e. natural mortality caused by factors other than predation, is not well known or documented for fish in general nor are the processes contributing to it (Baur *et al.*, 2006; Bass *et al.*, 2007; Golubev, 2009; Gislason *et al.*, 2010; Partridge, 2010). Several small, short-lived fish species have adult natural mortalities of more than 0.6 that increase with age (e.g. Gislason *et al.*, 2010). The increase in M with age during the adult life stage is, however, not well investigated for fish because it is difficult to isolate M from fishing mortality (F), but it has been documented for some stocks of small fish species (Beverton, 1963; Caputo *et al.*, 2002; Cook, 2004; Terzibasi *et al.*, 2007; Golubev, 2009; Uriarte *et al.*, 2010). For several fish species, there is evidence of residual mortality as a result of active gene-directed and age-determined apoptosis, senescence, and diseases associated with spawning. For some short-lived fish species, this is associated with truncated ontogeny, accelerated gonad maturation, and spawning events (e.g. Caputo *et al.*, 2002; Terzibasi *et al.*, 2007). Mediterranean goby (*Aphia minuta*) seems to have an endogeneous timer-inducing adult mortality immediately after the first spawning season by causing irreversible intestinal deterioration (Caputo *et al.*, 2002). Age-dependent degeneration or the dysfunction of several organs and age-related pathological changes similar to those of mammals has been demonstrated for a variety of fish species (Woodhead, 1998; Kishi *et al.*, 2003; Reznick *et al.*, 2006; Buston and Garcia, 2007). The short lifespan of the fish *Nothobranchius furzeri* is associated with explosive growth, accelerated sexual maturation, and the expression of ageing-genes causing behavioural and histological changes (Terzibasi *et al.*, 2007). Spawning mortality is observed for other small, short-lived fish species such as capelin (*Mallotus villosus*) and anchovy (*Engraulis encrasicolus*; Uriarte *et al.*, 2010) and suggested for Northeast Arctic cod (*G. morhua*), where males mature earlier and have higher mature mortality than females (Jakobsen and Ajiad, 1999). Indirect spawning-related mortality may also originate from the abrupt and substantial energy loss with increased vulnerability and exposure to invertebrate scavengers and predators. However, to our knowledge, it has not been reported for small species of the Gadidae family. In the North Sea, small gadoids, such as blue whiting (*Micromesistius poutassou*), poor cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*), silvery cod (*Gadiculus argenteus*), and NP, have been observed living up to ages 10–20, 5, 4, 3, and 5 years, respectively (www.fishbase.org), indicating that spawning stress and mortality might be an issue for some of these species.

Previously, data had been inadequate to investigate these dynamics for NP; however, there is a unique opportunity to estimate M for this normally exploited stock because fishing activity has been very low since 2003. The targeted fishery was totally closed in 2005 and 2007 as well as for the first half of 2006 because of a low stock level. In those periods, M approximately equals total mortality (Z).

It is essential, for both ecosystem and single-stock management, to investigate the natural mortality dynamics of NP, the periodical variability herein, and to provide accurate data on life-history traits influencing mortality rates used in ICES analytical assessments. Therefore, it is important to know whether this small gadoid species dies abruptly and at a relatively young age from spawning stress (e.g. Ursin, 1963; Bailey and Kunzlik, 1984; Lambert *et al.*, 2009) and energy depletion, similar to some salmon species, capelin, anchovies, and gobies, or if there are other reasons for which they have a short lifespan. In the study by Lambert *et al.* (2009), maturity and growth dynamics were thoroughly investigated. In the present paper, we analyse the level of natural mortality in relation to maturity, sex, and growth dynamics on quarterly and geographically disaggregated bases. This is done by the use of long-term data time-series in an effort to understand the mechanisms behind the dynamics of mortality, including predation and fishing mortality. Lambert *et al.* (2009) and the present study have different objectives, but overlapping documentation, and some figures from Lambert *et al.* (2009) have, therefore, been used in the present study. We tested three null hypotheses: (i) $H_0$1: natural mortality is constant over years (at a level of approximately $M = 1.6$) and quarters ($M = 0.4$) and independent of age; (ii) $H_0$2: there is no relationship between natural mortality and reproduction-specific life-history traits of NP, such as sex, maturity, or growth and, thus, mortality is decoupled from spawning; and (iii) $H_0$3: there is no density-dependence, neither intra- nor interspecific, in NP mortality.

Material and methods

To complete the objectives of this study, extensive disaggregated data were used, involving complex data compilation, manipulation, and analyses (see also Lambert *et al.*, 2009). The yearly abundance indices were computed from survey raw catch per unit effort (cpue) data by fish length combined with raw sex–maturity age–length keys (SMALKs). Data were available from the ICES coordinated International Bottom Trawl Survey (IBTS) for 1983–2006 covering the North Sea and Skagerrak–Kattegat (Anon., 2004). These indices were stratified by roundfish areas (RFAs) 1, 2, 3, 4, 7, 8, and 9 (see RFAs in Figure 1 in Lambert *et al.*, 2009). The total area differs and is wider than the combined index area covered for the standard calculation of the ICES IBTS abundance indices to assure the coverage of the full NP stock distribution area needed for the area-disaggregated analyses of geographical variability (Anon., 2001, 2004; Sparholt *et al.*, 2002a, b; ICES, 2004, 2007a, b, c). The NP stock is distributed mainly in the northern North Sea, Skagerrak, and Kattegat, and potential seasonal migrations do not result in the migration out of this shelf area because the NP stock is not distributed in areas with depths greater than 200–250 m (Sparholt *et al.*, 2002a, b). Data manipulation was necessary to perform the analyses of geographical variation because the SMALKs were not always complete for all areas for every year and quarter (i.e. for each cell). The initial data were taken from the ICES DATRAS database, and where information was missing, empty cells were filled with estimates based on the methods given in the IBTS manual and on biological and ecological knowledge (Anon., 2001, 2004; ICES 2007d). Such data filling was necessary in the SMALKs because there was a risk to bias data and results if valid and available cpue information were excluded from cells and not used in the analyses because there were no SMALK observations for these cells (Hoenig and Heisey, 1987). The manual provides standard substitution procedures for converting length data to age data when age–length keys (ALKs) are missing (for one RFA, 1 year, and one quarter) or are not reliable (e.g. an RFA with $<$ 25 otoliths sampled). Following the IBTS manual, the ALKs of certain RFA were used to replace the missing observations of the neighbouring RFAs in

a given quarter and year, when needed. However, the same procedure for converting data to sex and maturity data used in Lambert *et al.* (2009) was not adequate for the present study because of the spawning migration out of Skagerrak–Kattegat and its related sex distribution patterns (Ursin, 1963; Poulsen, 1968; Lambert *et al.*, 2009). Maturity ratios have proven variable between years (Lambert *et al.*, 2009), whereas sex patterns are more consistent. Consequently, the missing observations in the SALKs were replaced by the average of all available years for the same quarter and RFA. Therefore, total abundance indices, both in total and by sex, were computed following the procedure described by ICES (Anon., 2001).

Total mortality (Z) was calculated from the cpue values (Ricker, 1975; Sparre and Venema, 1989):

$$Z = \frac{1}{t_2 - t_1} \ln \frac{\text{cpue}(t_1)}{\text{cpue}(t_2)}, \quad (1)$$

where cpue is the catch in the number of individuals per trawl hour, and t_1 and t_2 represent ages, with $t_1 < t_2$.

To perform a robustness check and sensitivity analysis on the above described data-manipulation procedures for filling in gaps in SMALKs and SALKs, the yearly Z values by age were computed with Equation (1) using the revised area-disaggregated IBTS cpue data as described above (for age groups 1–4+) and compared with mortality estimates from abundance indices using the ICES standard calculation procedures and area. The comparison showed that the dynamics of the mortality from the revised cpue indices were very similar to those of ICES (Table 1). The present data compilation establishing more disaggregated data was thus determined to be valid and was preferred to investigate quarterly and sexual-disaggregated mortality patterns.

Table 1. Total mortality (Z) calculated based on IBTS cpue data according to ICES standard calculation procedures and according to the revised calculation procedure.

Cohort	Z_{1-2} ICES	Z_{1-2} (revised)	Z_{2-3} ICES	Z_{2-3} (revised)
1981	–	–	2.07	2.52
1982	0.83	0.84	2.60	2.56
1983	1.25	1.23	4.27	4.08
1984	1.81	1.74	1.84	1.91
1985	1.46	1.37	3.47	3.56
1986	1.48	1.38	1.43	1.58
1987	−0.72	−0.55	1.88	1.89
1988	0.99	1.03	1.75	1.35
1989	0.60	0.52	3.10	3.14
1990	1.02	0.96	1.23	1.26
1991	0.65	0.67	3.69	3.60
1992	1.97	1.89	1.58	1.53
1993	0.85	0.85	1.24	1.31
1994	0.81	0.84	1.37	1.44
1995	−0.47	0.26	1.72	1.75
1996	0.60	0.66	2.08	2.08
1997	0.53	0.60	2.22	2.14
1998	0.83	0.71	1.88	1.91
1999	1.04	1.02	1.18	1.18
2000	0.48	0.64	2.15	2.10
2001	1.14	1.00	2.83	2.81
2002	1.19	0.96	2.32	2.47
2003	1.92	1.79	1.58	1.81
2004	1.55	1.59	–	–

The disaggregated Z-values were, in a few cases, estimated to be negative, particularly from Q1 to Q2 and from Q3 to Q4, which is likely a consequence of incomplete spatial coverage in Q2 and Q4. ICES has evaluated the quality of the IBTS Q1 and Q3 to be high, and those quarters are estimated by ICES to be consistent with respect to coverage and catchability and are used in stock assessments (Fraser *et al.*, 2007; ICES, 2007a, b, c). Consequently, the indices from Q1 and Q3 were mainly used in this study.

For $H_0$1, the IBTS estimates of Z by age were compared with the MSVPA and SURBA model estimates (ICES, 2004, 2006, 2008) and to the estimates from Sparholt *et al.* (2002a) to evaluate seasonal and long-term trends in mortality as well as its age-dependence. Emphasis was placed on the more recent period when fishing activity, and fishing mortality were very low or zero in the NP fishery.

For $H_0$2, the evidence for linking mortality patterns to maturity and growth dynamics, i.e. indicating potential spawning mortality, was summarized based on Lambert *et al.* (2009). The mortality of mature individuals could not be computed directly because the percentage of fish maturing from one quarter to the next (from, e.g. histological studies) is unknown (Lambert *et al.*, 2009). Therefore, alternative multiple linear regressions and analyses of variances were performed to check for consistency between total mortality (Z) and sex and maturity ratios.

Concerning $H_0$3, variation in growth and maturity has been shown to be dependent on both intra- and interspecific densities (Lambert *et al.*, 2009). The mortality rates were consequently analysed in the context of variations in density. Linear regressions of Z as a function of the NP stock numbers and biomasses were tested and were also tested as a function of the spawning-stock biomasses (SSBs) of the main predator stocks of cod, saithe, haddock, mackerel, and whiting (ICES, 2007a, 2009).

Results

Magnitude and variability of mortality by age ($H_0$1)

Z by age does not show periodical trends over the period 1983–2006, except seasonal trends, and Z increases with age for all years (Figures 1 and 2; Supplementary material), i.e. both in years with and without targeted fishery, so the fishery cannot explain the difference. This age-dependent mortality is consistent for Z_{age3}, but the few exceptions here may be artefacts because of the scarcity of age group 4 individuals observed. For 2005, Z corresponds to M, because the fishery was closed in that year (Figure 1). Here, M_{age1} (1.59) is equivalent to the value used in the assessment, $Z = 1.6$. M_{age2} and M_{age3} are higher at 1.81 and 2.11, respectively. This age-dependent mortality confirms the conclusions obtained from the SURBA model analyses performed by ICES (ICES, 2004; Supplementary material) and from Sparholt *et al.* (2002a), while contradicting the MSVPA outputs indicating constant natural mortalities by age (ICES, 2004, 2006, 2007a, 2008). Both the 2008 and the ICES WGSAM 2011 results show some annual variability in the rate of mortality by predation (M_2), but a similar level for M_2 at ages 1 and 2.

Dynamics of maturity, spawning time, and place in relation to mortality ($H_0$2)

From Lambert *et al.* (2009), we know that the ratio of mature individuals at ages 2 and 3 decreases from Q1, i.e. spawning time, to Q3 (Figures 2 and 13 in Lambert *et al.*, 2009). In addition, very few post-spawning fish have been recorded despite extensive

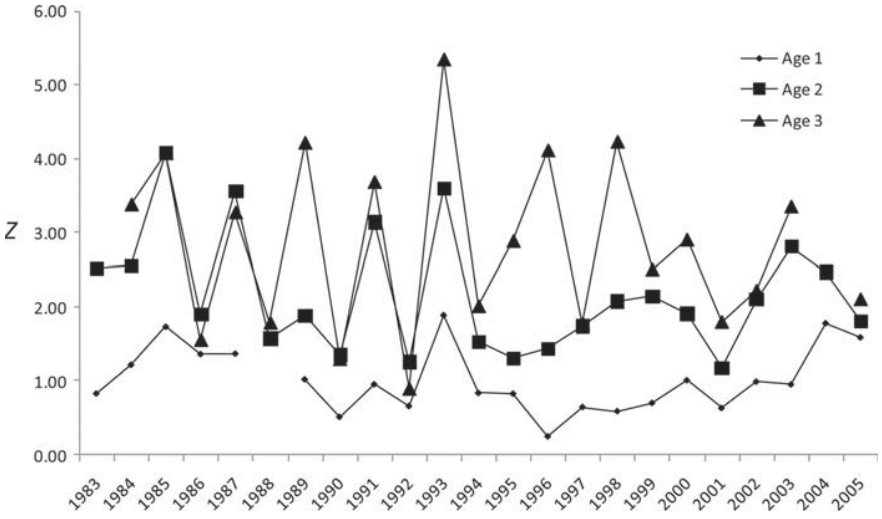

Figure 1. Total mortality (Z) by age over a 23-year period calculated according to Equation (1) based on revised IBTS Q1 cpue data. The negative value from 1988 age 1 was omitted from the calculation.

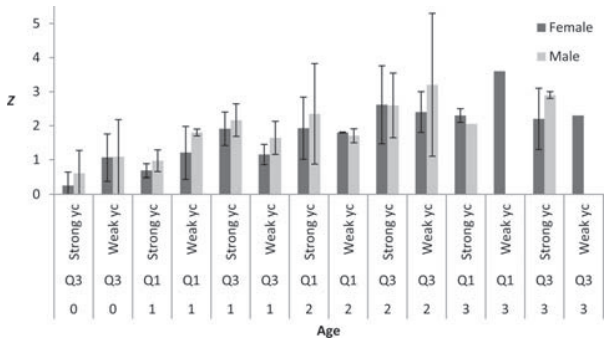

Figure 2. Seasonal total mortalities (Z) by sex and age for strong and weak year classes based on revised IBTS Q1 and Q3 cpue data. Z is calculated according to Equation (1). Error bars represent the standard deviations.

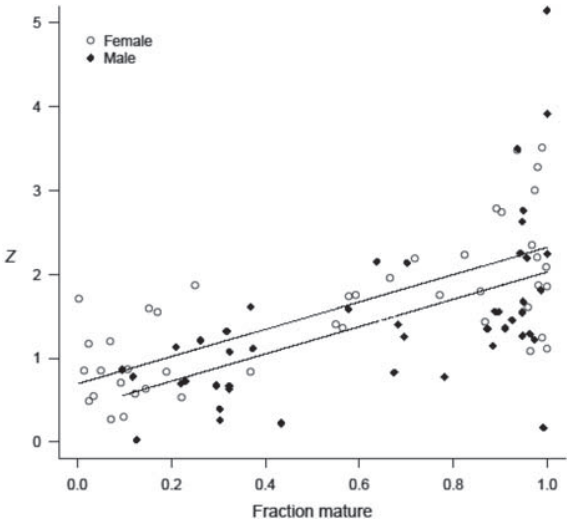

Figure 3. Total mortality (Z) of females (black dots) and males (white dots) as a function of the fraction mature for age groups 1 and 2. Z is calculated according to Equation (1) and based on the revised IBTS cpue data. Regression *t*-test statistics: $p < 0.001$ for females and $p = 0.058$ for males.

survey efforts, indicating a high mortality of mature individuals following the spawning event (Figure 2 in Lambert *et al.*, 2009). The maturity ratio also increases with age for both sexes and shows a strong spatial pattern, reflecting likely effects of spawning, as explained below (Figures 2, 3, 13, and 14 and Table 3 in Lambert *et al.*, 2009). Spawning areas of the NP stock are identified in Lambert *et al.* (2009), and the percentage of mature individuals is significantly higher in the main spawning areas RFA1 and RFA3, where the decrease in the maturity ratio from Q1 to Q3 is most evident (Figures 3 and 13 and Table 3 in Lambert *et al.*, 2009). This strongly indicates a link between spawning and greater mortality during the breeding season, i.e. direct or indirect mortality caused by spawning stress. Although mortality cannot be directly calculated for the spawning areas during and just after the spawning period, the yearly total mortality for both sexes is positively correlated with the overall maturity ratio assessed during the spawning season (Figure 3 and Table 2; Figures 2, 3, and 13–15 and Table 3 in Lambert *et al.*, 2009). Figure 3 shows a low mortality rate by sex until ~50% of the individuals are mature (with an unexplained gap between 0.4 and 0.6), a much higher rate above 60% are mature, and a very high level above 90% are mature. The spread around the latter high level indicates that some other factors apart from the fraction mature potentially influence mortality.

Growth dynamics in relation to mortality ($H_0$2)

The growth of NP shows strong spatio–temporal differences (Figure 8 and Table 5 in Lambert *et al.*, 2009). Body weight is generally stable from Q1 to Q2, with a notable exception found in the western North Sea, where age group 2 loses considerable weight. This is likely to be spawning-related because this area covers the main spawning ground of the stock. Besides the loss in weight, a general decline in mean length-at-age from Q1 to Q2 is also

Table 2. Statistics: *F*-test and the corresponding *p*-values of the multiple linear regression of total mortality (Z) from Q1 vs. sex and fraction mature.

	Estimate	s.d.	*t*-value	$p(>\|t\|)$
Intercept	0.69	0.16	4.38	<0.001
Sex: female	−0.29	0.15	−1.92	0.06
Fraction mature	1.63	0.21	7.61	<0.001

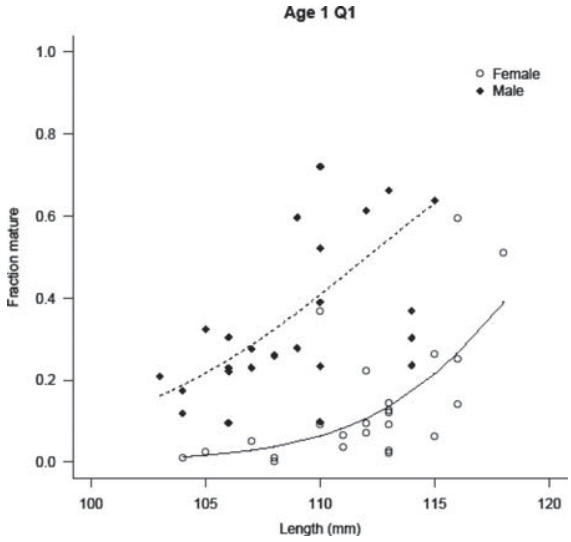

Figure 4. Relationship between the fraction mature and the mean length-at-age MLA (A1 Q1; males, $p < 0.001$; females, $p < 0.001$). Females, white dots and continuous curves; males, black dots and dashed curves (from Lambert *et al.*, 2009).

observed for both females and males (Figure 8 and Table 5 in Lambert *et al.*, 2009), implying that the proportion of large individuals has decreased from before to after spawning.

Integrated growth and maturity patterns in relation to mortality ($H_0$2)

When recruits benefit from favourable growth conditions during their first year, i.e. reach relatively large mean length at age 1 in the first quarter (MLA1 Q1), more individuals will mature before the spawning season (Figure 4). This clear pattern is observed for both females and males. Males mature earlier and at smaller sizes than females (Figure 5). Consequently, males form the major part of the spawning stock during the first spawning season of a cohort. This pattern coincides with the age 1 and 2 mortalities for males being higher than for females in Q1 (Figure 2), where males undergo a significantly greater mortality than females by an average of 0.2 (paired *t*-test, $t = 3.059$, d.f. = 101, $p = 0.003$), potentially explained by spawning-associated mortality.

Density-dependence in mortality related to density-dependence in maturity and growth ($H_0$3)

Early ages of less abundant cohorts show consistently higher mean mortality rates than the more abundant cohorts of both sexes, although the standard deviations are too high for this difference to be statistically significant (Figure 2). The negative relationship between year-class strength and the mortality rate of young age groups was investigated further. It appears that total mortality of age 1 males and females (Figure 6) tends to be lower when density is higher, although not significantly. No intraspecific relationship between mortality and density was observed for age 2 or 3.

The decreasing pattern in mortality in relation to intraspecific density over time (Figure 6) is unlikely to be caused by predation, even if it is generally accepted that higher prey density usually results in overall lower predation mortality (ICES, 2006, 2008). No significant interspecific density-dependence in *Z* for age 1 or 2 was found in relation to SSB for the most important predator stocks in the North Sea known to prey upon NP (ICES, 2006, 2008), i.e. saithe, haddock, cod, and whiting (Figure 7), nor has this been found for *Z* by sex (not shown). A general pattern indicates that mortality tends to increase when the main predator stocks become more abundant (Figure 7). However, this is not significant, and no seasonal patterns have been found to explain the quarterly patterns observed in the increasing mortality by age (Figure 2).

Lambert *et al.* (2009) showed that the maturity rates of age 1 NP were also negatively influenced by density (Figures 5 and 15 in Lambert *et al.*, 2009). The age and the length at which 50% of the fish are mature increase with increasing recruitment (Figure 18 in Lambert *et al.*, 2009). Variations in natural mortality can consequently be explained by spawning mortality, i.e. maturity occurs later and, thus, spawning mortality is lower at high population densities.

This correlation is supported by the relationships between growth, density, and mortality. The mean length at age 1 (MLA1) Q1 is negatively correlated with density (Figure 8), and MLA1 Q1 is lower for strong year classes (female, $p = 0.05$; male, $p = 0.03$). At age 2, the decrease is only significant for females ($p = 0.04$).

Discussion

$H_0$1: natural mortality is constant over years and quarters and independent of age

This hypothesis is rejected. The present study shows that the annual NP total mortality *Z* varied over the last 25 years, but no overall periodical trend could be observed except seasonal variation. There is a distinct and consistent age difference in *Z*. *Z* increases significantly with age and, based on Sparholt *et al.* (2002a), the peak in the length distribution representing larger individuals disappears between Q1 and Q2. The total mortality from 2005 to 2006 shows the same age pattern as for the full period investigated in the present study, i.e. mortality increases from ages 1 to 3. For these years, mortality corresponds to the actual natural mortality because the fishery was closed at that time. Both in historical times of relatively higher fishing mortality and in the most recent years of low fishing intensity, total mortality was highest for the oldest fish. Consequently, the effect of higher fishing activity on the oldest age groups cannot explain the observed trend. Furthermore, fishing intensity and mortality (ICES, 2010) in the directed NP fishery are actually highest in Q3 and Q4, which cannot explain the higher *Z* in Q1 and Q2 (Lambert *et al.*, 2009), i.e. the seasonal patterns in *Z*. Also, no sex-selective fishery was evident from the biological sampling from the fishery (not shown) that would explain the sexual differences

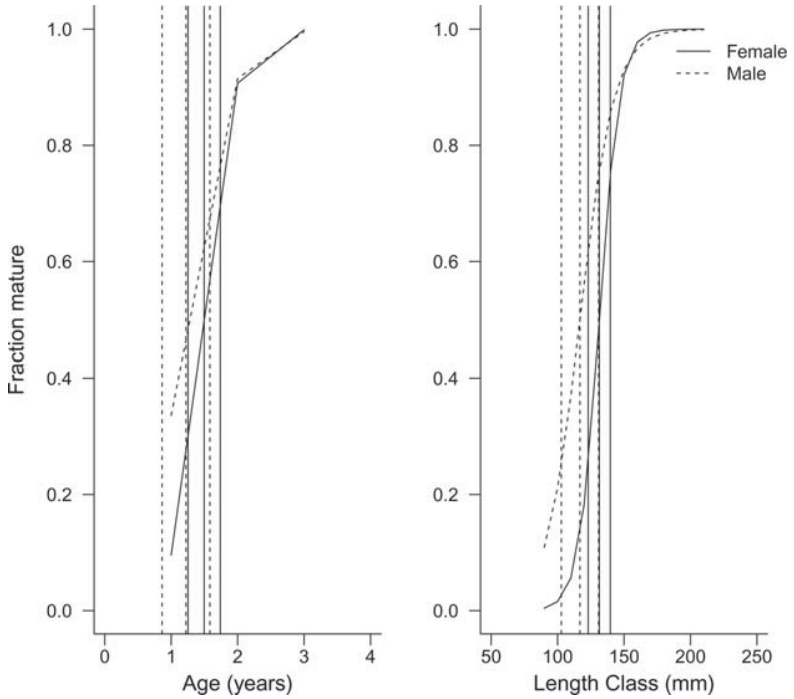

Figure 5. Fraction mature as functions of age [logit(p) = $a + b \times$ age] (left) and length [logit(p) = $a + b \times$ length] (right). Females, continuous lines; males, dashed lines; LC, length class. Vertical lines represent the age at 25, 50, and 75% maturity (from Lambert *et al.*, 2009).

observed in Z. Estimates of Z at age with confidence limits from a stock assessment with the full population dynamic SURBAR model (SURBA standard ICES assessment model in the statistical software R) based on IBTS Q1 and Q3 NP cpue data at age confirm the increasing mortality with increasing age (Supplementary Figure S1). Bootstrap analyses of observation variability (*CV*) in

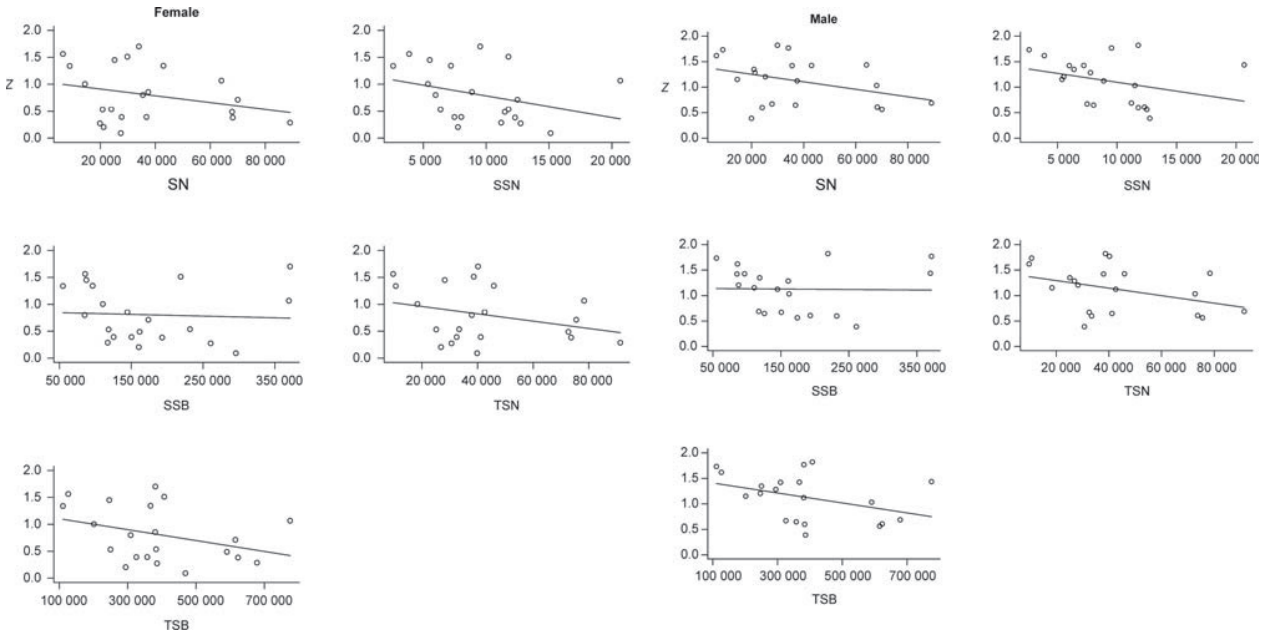

Figure 6. Total mortality (Z) based on revised IBTS Q1 cpue at age 1 vs. NP age 1 stock number (SN; $r^2_f = 0.08$, $p = 0.222$; $r^2_m = 0.14$, $p = 0.106$), spawning-stock number (SSN; $r^2_f = 0.11$, $p = 0.145$; $r^2_m = 0.10$, $p = 0.178$), SSB (t; $r^2_f = 0.00$, $p = 0.807$; $r^2_m = 0.00$, $p = 0.942$), total stock number (TSN; $r^2_f = 0.09$, $p = 0.177$; $r^2_m = 0.15$, $p = 0.096$), and total-stock biomass (TSB; t) ($r^2_f = 0.12$, $p = 0.117$; $r^2_m = 0.15$, $p = 0.089$). Female figures at left, and male figures at right; regression lines are shown; numbers in millions and biomass in tonnes (t). Z is calculated according to Equation (1).

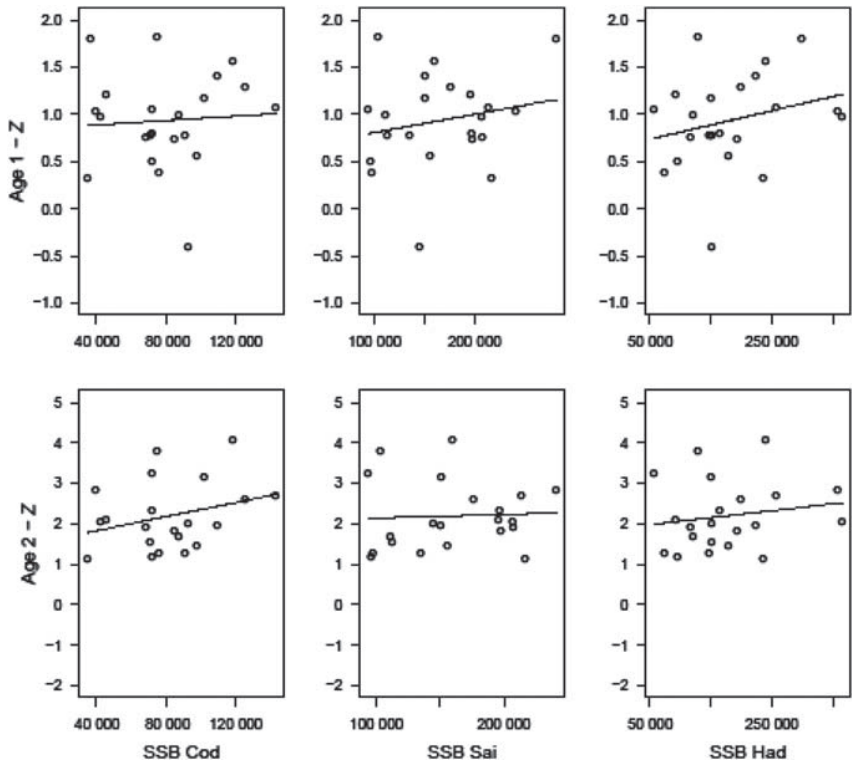

Figure 7. Total mortality (Z) based on revised IBTS Q1 cpue at age 1 (top panels) and age 2 (bottom panels) vs. SSBs (t) of three main predators on 1 January. Regression lines of the relationships shown for cod (Cod; age 1, $r^2 = 0$; age 2, $r^2 = 0.08$), saithe (Sai; age 1, $r^2 = 0.04$; age 2, $r^2 = 0$), and haddock (Had; age 1, $r^2 = 0.06$; age 2, $r^2 = 0.03$). Z is calculated according to Equation (1).

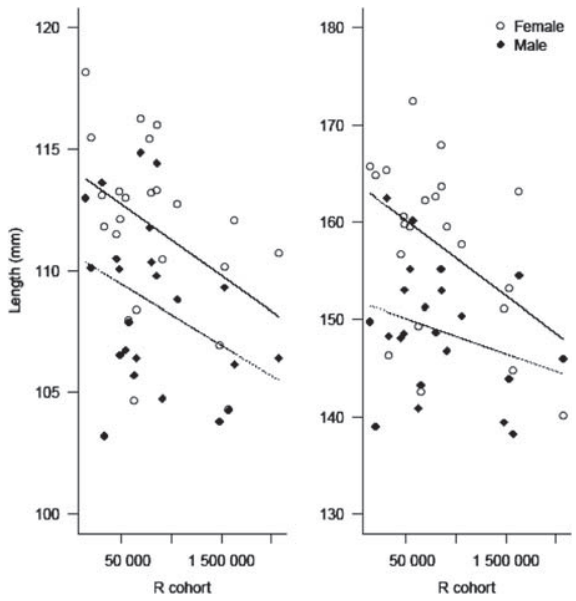

Figure 8. Mean length-at-age in Q1 of age 1 (left) and of age 2 in Q1 (right) vs. year-class strength [recruitment (R) of a cohort] showing statistically significant intraspecific density-dependence. Females, white circles and continuous lines; males, black dots and dashed lines; cohorts in millions (from Lambert *et al.*, 2009).

the same data support the differences in Z at age not being just random variability (Supplementary Table S1). In brief, the observed significant age- and season-specific mortality patterns can be directly explained by greater mortality associated with the spawning event for older fish in the first part of the year.

Survey coverage and catchability with respect to the hypotheses $H_0 1 - H_0 3$

A potential problem resulting from the use of survey results is that the sample size is generally small, and hence the abundance estimates are likely to be noisy (Cook, 1997). However, the survey time-series used in the present study have extensive coverage, and enough individuals have been sampled to obtain statistically significant results. ICES has evaluated the IBTS Q1 and Q3 and has concluded that they have adequate coverage and consistent time-series information for use in NP stock assessments (ICES, 2007a, b, c, d). These data are widely used in similar fish population dynamic analyses on NP and other demersal, gadoid species (e.g. Cook, 1997; Cotter, 2001; Beare *et al.*, 2002; Lambert *et al.*, 2009). The robustness and sensitivity analysis of potential data compilation effects of SMALKs to include all available cpue data for a wider area showed similar dynamics of the mortalities calculated from the revised cpue indices compared with those from the ICES standard area. In both cases, the ICES standard calculation (summing and raising) procedures were used (Anon., 2001). The data filling has not been so extensive that it can influence

the overall results. Even if there were a potential effect, it would only affect the results and introduce noise concerning the geographically (spawning area) related analyses because the main data filling only concerned the geographical area disaggregation level.

The conclusions are based on the assumption that there is no significant difference or bias in NP catchability according to age (for the 1+ group) or year in the surveys, i.e. the sampling of each age group, especially the 1+ group, is representative for the stock. This assumption is assessed to be reasonable.

First of all, age group 1 NP has a mean length of 11–15 cm in Q1–Q4 varying with sex, maturity, and region (Lambert *et al.*, 2009), and the observed length range of age 1 in the full IBTS Q1 ALK time-series is 5–17 cm, of which only 0.6% are <8 cm, 1.6% are 8–9 cm, and 6.5% are 9–10 cm (DATRAS, www.ices.dk). Götz (1997) published the only available selection parameters and ogive for NP in the IBTS GOV trawl, and she estimated an L_{50} of 8.0 cm, with a very narrow selection range, where 100% of the NP are caught at length 9.2 cm, the length where North Sea NP are fully selected by the IBTS survey gear.

Second, there is no indication in the literature of lower catchability of the older age groups for the species covered by the IBTS survey, including NP (Cook, 1997; Cotter, 2001; Beare *et al.*, 2002; Anon., 2004). Cotter (2001), Cook (1997), and Anon. (2004) have indicated that survey catchability of 0-group gadoids, clupeoids, etc. may, in general, be relatively low due to the mesh-size selection in the small-meshed IBTS survey trawls, but this is not the case for the 1+ group. Cook (1997) found that the small gadoid whiting has equal catchability for all ages 1–6 in the IBTS survey. Furthermore, neither the surveys nor the commercial fleet have been able to find old NP (see below). Fraser *et al.* (2007) calculated the IBTS survey (GOV-trawl) catchability for NP. The results showed a constant catchability for NP in the length interval 12–20 cm, and the catchability was low for small fish of ~7.5 cm (the 0-group), which is similar to the length of the estimated L_{50} for NP for the GOV trawl (Götz, 1997). Fraser *et al.* (2007) estimated lower IBTS catchability for fish of lengths of ~20–23 cm. However, the confidence limits for this estimate were high and substantially overlapped those for the estimated catchability within the full size range 15–23 cm, i.e. this result was not significant. NP at age 2 has mean lengths of 12–15 cm (immature fish) and 15–18 cm (mature), whereas age 3 mean lengths are 14–16 and 18–20 cm for immature and mature fish, respectively (Lambert *et al.*, 2009). Therefore, the results of Fraser *et al.* (2007) did not indicate low IBTS catchability of the age and length groups for which we estimated high mortality, i.e. for ages 1–3.

Third, several scientists have suggested that the depth distribution of NP could increase with age (e.g. Poulsen, 1968; Raitt and Mason, 1968; Albert, 1994, in the Norwegian Deep). Sparholt *et al.* (2002a, b) analysed and discussed these potential catchability changes with age in relation to depth-dependent distribution and migration based on several sources, including IBTS data analyses and a literature review. They concluded that there was no evidence of vertical migration and associated age-specific migrations out of the NP population area and the IBTS area according to depth or topographical conditions, which could explain the very less number of old NP in the catches in the North Sea and Skagerak–Kattegat. Furthermore, Lambert *et al.* (2009) demonstrated that there is no basis for dividing the stock into several smaller stock components based on analyses of variability in growth and maturity dynamics. In addition to the work of Fraser *et al.* (2007), fishery landings statistics do not indicate depth differences between sizes, and the number of individuals found in deeper waters remains very low. Fishers have found no signs of emigration of the stock out of the area, and they have not noticed size- or age-specific patterns in occurrence according to depth either in the bank areas or along the Norwegian Trench (Flemming Christensen, a long-time NP fisher and former Chairman of the Danish Commercial Fishery Association, pers. comm.). Finally, papers (Cook, 1997; Cotter, 2001) and reports (Beare *et al.*, 2002; ICES, 2004) find similar trends in age-specific mortality using independent sources, i.e. different North Sea surveys and commercial fishery data time-series.

Consequently, age-, season-, and area-specific mortality patterns cannot be explained by survey coverage and catchability or by age-specific migration out of the area or vertical distribution patterns by age. We have no objective information indicating that larger NP (at least age 1+) are not representatively sampled in the analysed IBTS surveys and that the constant catchability assumption is not valid.

$H_0$2: there is no relationship between natural mortality and the reproduction-specific life-history traits of NP, such as sex, maturity, and growth, and thus, mortality is decoupled from spawning

This hypothesis is also rejected. The present study and Lambert *et al.* (2009) provide evidence that spawning mortality impacts the life-history traits and population dynamics of the NP stock. The ratio of mature individuals declines significantly from before to after spawning, and only very few post-spawning NP have ever been observed despite extensive surveying and fishing in the North Sea. For the youngest age classes, the proportion of mature individuals is higher for males than for females, and total male mortality is higher. This is in accordance with Cooper (1983), who found an increasing numerical dominance of NP females with age. Maturity and growth dynamics (Lambert *et al.*, 2009) strongly indicate greater mortality in the spawning areas and during the spawning season, as further discussed below.

Geographical patterns and mortality dynamics pertaining to $H_0$2 and $H_0$3

Geographical patterns and subarea-dependent mortality have not been explored to the fullest extent in the present study using IBTS data because potential patterns therein might be flawed by subarea-specific NP migrations within the North Sea and Skagerrak–Kattegat. Although such internal migration patterns are not fully mapped, it is clear that Skagerrak–Kattegat is a nursery area and that NP migrate to the North Sea when maturing (Ursin, 1963; Poulsen, 1968; Lambert *et al.*, 2009). Geographically determined growth patterns of decreasing mean weight and length with age in the spawning areas during the spawning season have been observed (Lambert *et al.*, 2009). In addition, geographical maturity patterns have shown a significantly higher percentage of mature individuals in spawning areas RFA1 and RFA3, in which there were significant decreases in the maturity ratio from Q1 to Q3, and where more than 90% of the spawners were recorded in Q1 (present study and Figures 2 and 3 and Table 3 in Lambert *et al.*, 2009). This indicates that the larger, more mature individuals disappear after spawning. It is also observed

that total mortality is significantly correlated with the percentage of mature fish. Mortality cannot be directly calculated in the spawning areas during and just after the spawning period, but the results show that the yearly total mortality for both sexes is significantly positively correlated with the overall maturity ratio assessed during the spawning season (Figure 3). The above factors indicate a higher natural mortality associated with spawning.

Based on stomach-content data analyses disaggregated to ICES statistical square (area) and quarter of the year in the North Sea (1991), Rindorf *et al.* (2010) calculated biomass eaten and local predation mortality indices. They found that predated biomass (and predation mortality) of NP by cod, whiting, haddock, and saithe was high in the second half of the year (Q4 and Q3) and low in the first half (Q2 and Q1). In Q1, the small NP biomass eaten occurred in the most northern areas west of Orkney and south of Shetland. Based on Rindorf *et al.* (2010, Figures 2b and 5b), the areas of highest biomass predated and highest predation mortality were not in the main spawning areas during the spawning season (Q1) that were identified by Lambert *et al.* (2009, e.g. Figure 1). The latter study includes a review of previous studies on NP spawning and egg/larvae distribution and identifies the main NP spawning areas to be in proximity to the 120-m isobaths in RFA1 and RFA3 near Viking Bank along the Norwegian Trench and along the Scottish east coast (and in RFA7) in Q1. Consequently, predated biomass and predation mortality are low in the main spawning areas and during the spawning season, indicating that increased mortality cannot be explained by predation mortality.

$H_0$3: there is no density-dependence, intraspecific, or interspecific mortality in NP

This hypothesis cannot be conclusively rejected. The density-dependence, either intra- or interspecific, of NP mortality shows a distinct pattern. Mortality is significantly positively correlated with intraspecific population density. The NP population dynamics seem, therefore, to be influenced by density-dependence, which results in a lower growth rate and maturation when the stock is at a relatively high level. Thus, bringing together the varied information pertaining to NP mortality, it is likely that lower stock densities contribute to higher growth rates and higher maturity ratios and, consequently, greater mortality rates, which are most likely caused by spawning. Kempf *et al.* (2009) found no intraspecific relationship between NP SSB in the year of birth and the IBTS age 1 recruitment index of the following year, whereas the interannual variability in age 1 recruitment was found to be correlated with the Q2 sea surface temperature when taking predation impact into consideration. However, this was not highly significant and included the removal of years characterized as outliers.

Interspecific density-dependence and predation were not significant factors based on the available data at the scale of our study, but additional studies are necessary on more disaggregated coverage and overlapping distribution and density patterns between NP and its main predators by age or size group, especially during the spawning period. With regard to the overlap between NP and important predators in the North Sea, Rindorf *et al.* (2010) found low predated biomass and predation mortality in the main spawning areas during the spawning season. Kempf *et al.* (2009; Figure 10) found no strong correlation between the spatial overlap of NP age 1 abundance and certain NP predators (saithe, haddock, and mackerel) in the IBTS Q3 survey. Both of these studies are based on extrapolations of the 1991 "Year of the Stomach Sampling" diet compositions of predators. However, strong predator–prey relationships do exist between some commercially important North Sea stocks and NP. Adult whiting is an important predator of small NP (Jones, 1954; Daan and Welleman, 1998). In recent years, a significant part of the western mackerel stock has migrated to the North Sea, resulting in a potential higher predation mortality of small/young NP (particularly of the 0-group). Further, the North Sea saithe stock has recently increased, leading to potentially higher predation mortality among larger NP (ICES, 2010). The stomach contents of the main predators should be analysed for the years beyond 1991 (ICES, 2006, 2008; Kempf *et al.*, 2009; Rindorf *et al.*, 2010) at the precise NP spawning time and place to determine whether NP are subject to increased predation when potentially weakened by spawning events.

Although our analyses indicate density-dependent mortality which can be associated with spawning and that available documentation on predation cannot explain the observed increase in Z at age, it is difficult to disentangle density-dependent mortality and size-selective mortality. Size-selective mortality will usually result in greater mortality of the smallest (youngest) fish, but for NP, we observe greater mortality rates for the largest (oldest) fish, and that spawning is not only associated with age, but also with size. We find evidence of spawning mortality where the fastest growing individuals mature faster and therefore spawn and die faster, but there may be other reasons for such reversal size-selective mortality, e.g. density-dependence. Density-dependence probably does not influence mortality directly, but rather indirectly as explained above, and can also be influenced by size-selective mortality other than spawning mortality, so no rigorous conclusions can be made on the rejection of hypothesis $H_0$3.

Conclusions and future studies

Our results indicate that a significant proportion of the NP stock most likely dies as a direct or indirect result of spawning. However, the variation in total mortality is high and cannot be exclusively explained by this one life-history trait, i.e. other types of size-selective mortality may also have an effect. In fisheries and ecosystem management, it is important to recognize the biological and ecological contexts and mechanisms that lead this small, short-lived gadoid to allocate so much energy to reproduction the first time it spawns and to produce a high likelihood of death as a result of spawning stress or increased exposure to other mortality associated with spawning. Ursin's (1963) studies on NP growth have indicated that a likely cause of the observed growth and energy allocation dynamics may be the mortality associated with spawning.

With respect to NP, future investigations should concentrate on (i) intensified surveying of NP and its predators during and just after the spawning event at the spawning localities to follow mortality and predation patterns, (ii) precise maturity patterns and histological gonad analyses during the spawning season to follow the mortality patterns of NP that are closely associated with development in the mature stages before and after spawning, (iii) histological analyses of NP gonads and other organs in relation to potential senescence associated with spawning, and (iv) tank experiments on spawning NP. With these approaches, it will be possible to evaluate some mortality mechanisms and to what

extent NP is weakened by the spawning event due to energy loss and increased vulnerability and exposure to fish and invertebrate predation, as well as senescence, sickness, and other residual mortality induced by spawning.

Supplementary material

The following supplementary material is available at the *ICESJMS* online version of the manuscript: bootstrap analysis and estimation of observation variability (*CV*) in the NP IBTS Q1 and Q3 cpue data by age, and total mortality (*Z*) at age with confidence limits from a SURBAR full population dynamic model assessment in 2011.

Acknowledgements

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Chapter 5

Development, use and analysis of integrated survey information to describe Western Baltic herring occurrence in the Sound associated with stock feeding and spawning migration patterns

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Distribution, density and abundance of the western Baltic herring (*Clupea harengus*) in the Sound (ICES Subdivision 23) in relation to hydrographical features

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Abstract

Biomass and duration of the over-wintering period of the Rügen spring spawning herring stock (RHS) in the Sound (ICES Subdivison 23) were investigated as well as possible hydrographical factors affecting relative distribution and triggering southwards migration towards the spawning grounds. Monitoring was performed during 27 surveys over a 6-year period (1993–1998). Abundance of 45–165 000 t in August–February, 5–60 000 t in March–May, and <2000 t in June–July was found. This indicates a longer over-wintering period than hitherto assumed. The year classes 1988, 1991 and 1994 were relatively strong occurring in the Sound from age 2 (winter-rings) and abundance in autumn 1993 and 1996–1997 was relatively high. Relative year class strengths are in accordance with variations in larval indices at the spawning grounds. Decreasing abundance in late spring in the Sound was concordant with observed peaks in commercial landings and (subsequent) peak larval indices at the spawning grounds. Larger size groups seem to migrate southwards in spring before smaller herring size groups. Peak herring densities occur in the northern Sound in autumn and they do not concentrate near the southern Drogden threshold in spring before southwards spawning migration. Highest densities were found from 8 to 22 m below sea surface, and just below or in the halocline in areas with stratified water column. Indications of inflows to the Baltic triggering southwards migration can be observed at some occasions, however, these results are not conclusive because of relatively few biomass estimates in 1996–1998. The identified patterns in herring occurrence agree with some conclusions on migration routes for RHS from previously reported tagging studies, but the present investigations indicate prolonged over-wintering in the Sound. This report quantifies the abundance and distribution of herring in the Sound over the year on basis of repeated investigations, and investigates possible influence of hydrographical factors on distribution and migration.

Keywords: Abundance; *Clupea harengus*; Density; Distribution; Herring; Hydrographical features; ICES Subdivision 23; Over-wintering period; Rügen herring stock; The Sound

1. Introduction

The Sound (ICES Subdivision 23) is a transition area between the Baltic Sea and Skagerrak/Kattegat for several important migrating fish stocks including herring (*Clupea harengus*), garfish (*Belone belone*),

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lumpsucker (*Cyclopterus lumpus*), mackerel (*Scomber scombrus*), and to some extent cod (*Gadus morhua*) (ICES, 1989). Among these the spring spawning Rügen (western Baltic) herring stock (RHS) is a significant resource for the Danish, German, Norwegian and Swedish commercial fishery in the Baltic Sea, Kattegat/Skagerak, and to a lesser extent in the North Sea (ICES, 1998).

Results from tagging experiments and fishery information (Biester, 1979a,b; Jönsson and Biester, 1981; ICES, 1983a; Otterlind, 1984, 1987; Aro, 1989) indicate that the Sound is a major over-wintering area for the RHS, and that the main component of herring in the Sound is RHS. These studies showed a typical migration pattern of RHS between the main spawning grounds around Griefswalder Bodden to the feeding areas, one north-westward migration extending to the Kattegat/Skagerrak/North Sea area and one eastern migration extending to about 16°E in the Baltic Sea east of Bornholm and the western part of Hanö Bay. This information is, however, only qualitative and indicative (sometimes anecdotal) as well as relatively old and may not reflect the present stock situation and migration patterns. No detailed, quantitative investigations of occurrence and abundance of the over-wintering RHS in the Sound, and the passage of migrating herring through the Sound, have previously been carried out on a seasonal basis over the year for a period of several years. There is a need to quantify the occurrence of herring over the year in different years and in different areas of the Sound to throw light upon the exchange between the south-western Baltic and Kattegat/Skagerrak and the yearly variation (ICES, 1983a; Otterlind, 1984).

During the period September 1993–May 1998, 27 hydroacoustic echo integration surveys with a standard set of acoustic transects were carried out in the central Sound from Helsingør-Helsingborg (north) to Drogden (south) covering all seasons of year. From concurrent biological sampling with scientific, multi-panel gillnets equipped with a wide range of mesh sizes and/or with large, pelagic trawls with fine meshed cod-ends, species composition and size and age were estimated. The results were compared with concurrently sampled hydrographical (CTD) data and data on water currents. In the present study the objectives of the analyses of the results from this sampling have been to investigate:

- Biomass levels of RHS in the Sound over several years in all seasons of year.
- Duration of the over-wintering period for the RHS in the Sound. The hypotheses were that RHS over-winter in the Sound from September/November to December/January (h:1), that the Sound is an important over-wintering area for the stock (h:2), and that the main herring component in the Sound is RHS (h:3).
- Specific distribution and density patterns of herring in relation to hydrographical features and depth in different areas, seasons of the year and between years in the Sound. The hypotheses were that during autumn and early winter the RHS concentrates in the deeper parts of the Sound below the pycnocline (h:4), and that in spring the RHS will concentrate in the southern part of the Sound close to the Drogden threshold (the shallow water area around Saltholm) before southwards migration to the spawning grounds (h:5).
- Whether water inflows to the Baltic may trigger southwards migration of RHS from the Sound to the spawning grounds. The hypothesis is that southwards migration indicated by declines in biomass levels of RHS in the Sound is directly correlated with longer periods of inflow to the Baltic (h:6).
- Which size groups of herring migrate southwards first. The hypothesis is that the largest herring start spawning migration first (h:7).

2. Materials and methods

2.1. Surveys performed

From September 1993 to May 1998, 27 hydroacoustic and 23 parallel gillnet surveys as well as eight parallel trawl surveys were carried out in the Sound. Table 1 gives an overview of survey activities.

2.2. Study and survey area

The survey area covers the central Sound and was divided into 13 geographical strata to describe small-scale geographical variations in herring occurrence (Fig. 1). Geographical coverage is shown in Fig. 2. Total survey area is approximately 280 square nautical mile and each stratum area (Fig. 1) was measured from

Table 1
Overview over survey activities, and density per geographical stratum (N/nm^2) of herring subdivided by survey and geographical strata. Total and mean biomass (BM) in tons (t) and abundance (N) in millions for the whole Sound area for each survey is presented

Survey period	S0193, September 1993	S0293, October 1993	S0393, December 1993	S0494, January 1994	S0594, February 1994	S0694, March 1994	S0794, April 1994	S1094, October 1994	S1194, November 1994	S1294, December 1994	S0195, January 1995	S0295, February 1995	S0395, March 1995	S0495, April 1995	S0595, May 1995	S0695, July 1995	S0795, August 1995	S0995, October 1995	S0196, March 1996	S0496, April 1996	S1096, October 1996	S1196, November 1996	S0397, March 1997	S0497, April 1997	S1197, November 1997	S0398, March 1998	S0598, May 1998
Overview of types and intensity of sampling																											
Acoustic integration	17/9–22/9	25/10–30/10	29/11–4/12	10/1–15/1	14/2–19/2	14/3–19/3	11/4–16/4	17/10–20/10	21/11–27/11	12/12–16/12	9/1–16/1	6/2–10/2	27/2–4/3	27/3–2/4	25/5, 30/5–31/5	10/7–11/7	6/8–11/8	9/10–13/10	18/3–22/3	10/4–14/4	30/9–6/10	11/11–17/11	3/3–9/3	5/4–10/4	11/11–15/11	30/3–3/4	17/5–19/5
Gillnet sampling	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×	×	×	×	×	×	×	×	×
Trawl sampling		×						×								×		×			×				×	×	×
Hydrographical sampling								×	×	×	×	×	×	×	×	×			×	×	×	×	×	×	×	×	×
Extended individual sampling		×		×				×		×		×		×					×		×	×	×	×	×	×	×
Herring density in number in millions per square nautical mile																											
Stratum																											
G01	6.48	3.71	–	–	–	–	0.17	2.20	0.33	2.22	0.61	0.20	1.79	0.27	0.27	0.23	6.55	1.51	1.70	1.08	1.24	16.23	1.74	3.71	12.78	10.57	0.99
G02	8.58	4.91	6.78	6.22	1.76	1.15	0.42	2.78	0.53	1.30	0.72	0.55	0.64	0.24	0.36	0.20	2.19	1.45	0.99	0.23	5.64	7.24	2.43	4.51	11.84	2.56	0.50
G03	7.54	5.54	6.57	9.94	13.78	1.47	0.86	2.79	0.49	2.81	1.39	0.52	0.84	0.39	0.25	0.15	3.29	2.56	1.39	0.78	1.62	7.19	4.72	6.02	10.77	6.71	0.45
G04	9.17	4.40	3.44	5.18	15.39	1.05	0.47	4.09	1.65	2.21	0.89	0.22	1.57	0.36	0.32	0.13	2.80	1.52	1.85	0.88	9.12	8.52	3.36	2.77	6.84	6.72	0.66
G05	3.05	3.50	1.78	2.36	3.78	0.62	0.15	2.30	1.24	1.09	1.12	0.23	0.38	0.30	0.57	0.22	1.41	1.75	1.12	0.63	3.05	3.09	3.82	2.80	4.78	3.59	0.47
G06	4.33	2.97	1.75	2.11	3.65	0.67	0.19	2.16	1.79	1.03	1.40	0.17	0.39	0.58	0.42	0.11	0.77	0.57	0.77	0.99	3.08	2.70	6.11	2.13	3.47	1.53	0.61
G07	3.71	1.91	2.16	1.60	0.71	0.78	0.10	1.49	1.31	0.83	0.62	0.21	0.42	0.73	0.28	0.07	1.34	0.53	0.97	0.16	5.42	1.67	2.13	2.05	3.19	1.15	0.53
G08	2.73	2.77	0.46	1.52	–	–	0.07	1.80	1.99	1.18	0.66	0.21	0.19	0.19	0.28	0.04	0.54	2.10	0.32	0.34	3.82	1.58	0.01	1.00	2.34	1.07	0.44
G09	3.32	3.05	3.06	0.83	0.82	–	0.04	2.54	1.09	0.96	1.18	0.31	0.14	0.16	0.27	0.03	0.75	0.67	0.35	0.19	1.82	1.18	0.01	0.71	1.68	0.28	0.38
G10	3.19	1.37	2.19	0.58	0.45	–	0.03	0.69	1.80	0.85	0.04	0.08	0.16	0.11	0.46	0.03	0.57	0.31	0.29	0.18	0.11	0.57	0.01	0.20	1.32	0.52	0.23
G11	1.50	2.32	1.85	0.91	0.03	–	0.02	0.23	0.30	0.50	0.03	0.03	0.35	0.06	–	0.01	0.14	0.25	0.16	0.06	0.07	0.04	0.01	0.02	0.02	0.06	0.06
G12	1.15	0.25	0.25	0.03	0.01	–	0.01	0.01	0.02	0.01	0.03	0.01	0.03	0.03	0.01	0.01	0.16	0.02	0.01	0.01	0.01	0.02	0.01	0.01	–	–	–
G13	–	–	–	–	–	–	–	0.01	0.01	0.01	–	–	–	–	0.01	0.01	–	–	–	–	–	–	–	–	–	–	–
Mean (by strata)	4.56	3.06	2.75	2.84	4.04	0.96	0.21	1.78	0.97	1.15	0.72	0.23	0.58	0.29	0.27	0.10	1.71	1.10	0.83	0.46	2.92	4.17	2.03	2.16	5.37	3.16	0.48
N:Sound, total	1151, 44	792, 08	680, 47	674, 29	835, 97	132, 02	51, 30	513, 32	320, 07	314, 88	205, 17	61, 42	127, 22	86, 91	82, 67	24, 80	370, 40	284, 93	207, 56	113, 07	839, 50	857, 73	553, 13	537, 45	1125, 67	608, 93	116, 48
Herring density in tons per square nautical mile																											
Mean (by strata)	438.85	319.38	248.54	309.55	421.85	107.58	22.19	283.55	150.85	191.51	112.36	31.33	79.97	38.17	35.38	6.92	297.55	176.42	138.20	76.24	295.85	390.04	211.36	223.33	733.89	287.48	29.42
Minimum (by strata)	148.38	30.56	30.63	5.09	2.22	90.93	1.44	0.98	1.92	2.63	5.68	0.65	3.60	4.28	–	0.08	24.71	2.73	1.97	1.09	1.82	2.56	0.01	0.77	2.87	11.72	3.70
Maximum (by strata)	715.31	469.32	443.30	855.59	1,414.19	139.30	80.91	556.36	345.46	464.24	208.84	85.26	238.04	96.71	70.45	22.62	1,109.92	401.64	341.93	162.32	667.90	1243.41	728.85	688.52	1615.28	800.28	60.19
BM:Sound, total	118832	87794	65462	77241	91061	15933	5609	83609	50049	50795	31395	8270	17703, 26	11511	10759, 33	1548, 38	65075	45690	34989	19069	90595	88404	58406	56554	163184	62144	7089

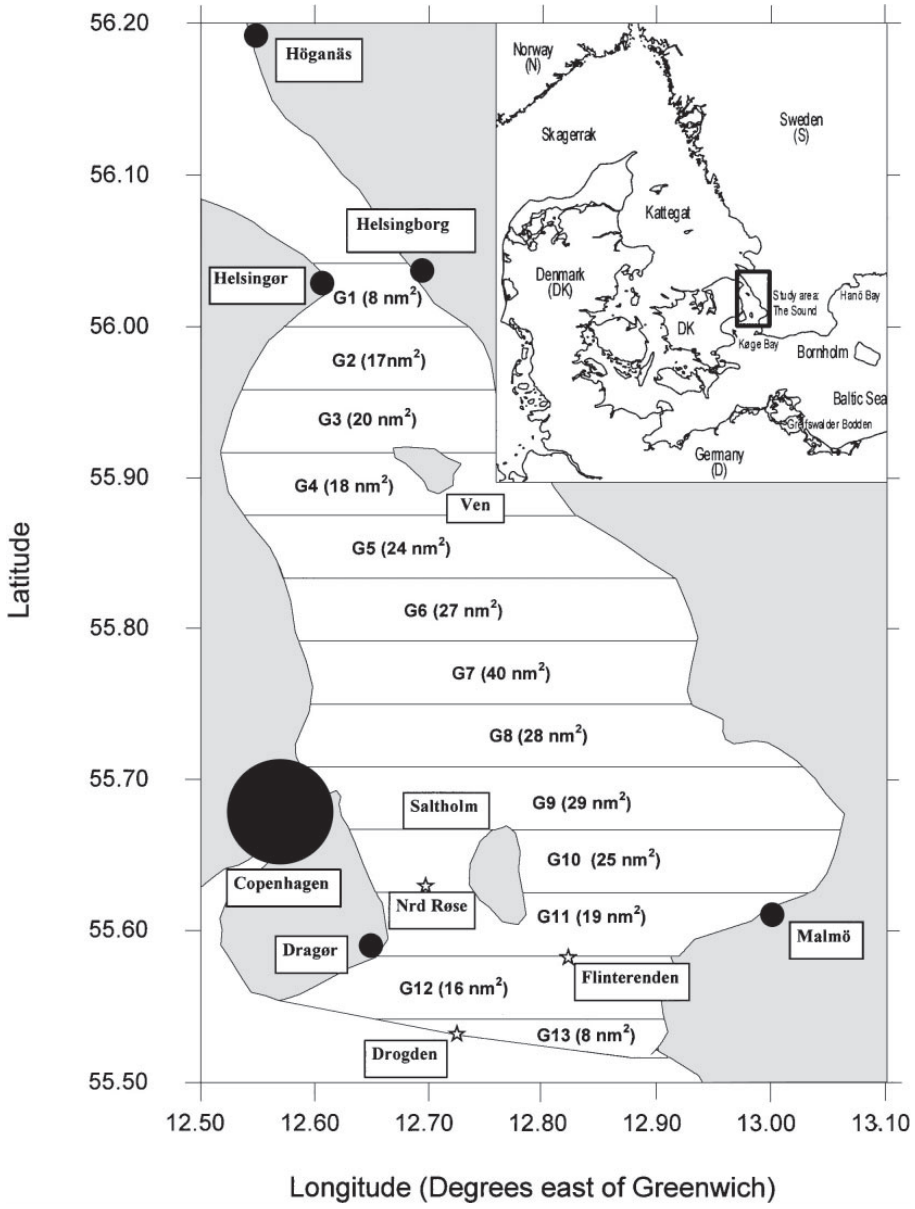

Fig. 1. Map over the survey area in the Sound (ICES Subdivision 23) by geographical stratum.

official Danish nautical navigation maps (The National Survey and Cadastre, Maps Int1331 and Int1332).

2.3. Collection of hydroacoustic echo integration data

Hydroacoustic echo integration was performed on each survey through standard transects (Fig. 2). Details of survey activities are given in Table 1. Echo integration was performed with a SIMRAD EY200 38 kHz single beam echo sounder system during all surveys except in May and July 1995, when a SIMRAD EK400 38 kHz single beam system was used. The transducer was mounted on a towed body. Towing depth was typically 2 m below sea surface to avoid disturbances from wind wave turbulence and air bubbles. The 3 m layer below the transducer was not included, because it is within the near-field zone of the transducer, which means no integration data are available in the 0–5 m depth layer. Experience from pilot-investigations, the present gillnet fishery and

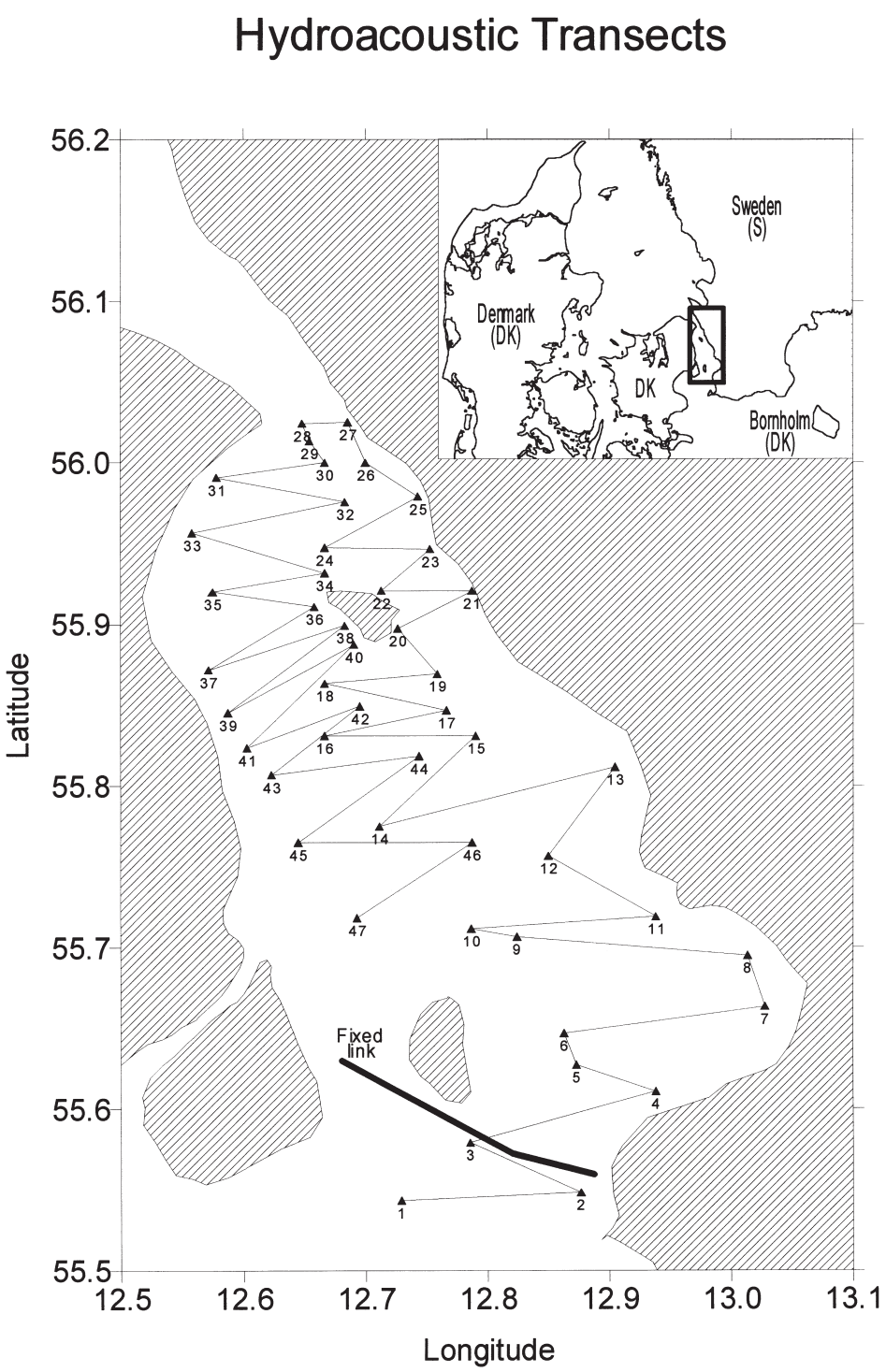

Fig. 2. Hydroacoustic transects in the survey area with waypoints for change of course shown.

from commercial gillnet fishery is that only a very small fraction of herring biomass occurs in the upper 5 m surface layer during the night in the Sound, and at localities with bottom depths less than 5 m. The survey track lines usually extended to well beyond the point where there were any clear indications of herring abundance left in the near shore areas. The echosounder systems were calibrated using the standard target method (Foote et al., 1986; Degnbol, 1988; Degnbol et al., 1990). Acoustic integration was per-

formed during darkness only, covering the standard zigzag transect pattern on each survey, but the order and direction in which individual transects were sailed, was chosen according to wind and current conditions. Surveying was done at night to avoid problems of fish aggregating close to or on the bottom which would make it difficult to separate fish echoes from bottom echoes. Another advantage of night measurements is that herring aggregations have dissolved, which means that errors due to fish in the upper part of the water column shadowing fish in the lower part of the water column or due to multiple scattering in the aggregations can be considered negligible (Foote, 1982, 1990). Acoustic data, time and GPS position data were stored, and later judged and analysed using the EchoAnn analyser system (Degnbol et al., 1990) according to procedures described in Appendix A. Horizontal and vertical contour plots of herring density in the Sound were made for each survey based on hydroacoustic data allocated to raised catch data (see below and Appendix A). Typical examples of plots from autumn and spring are shown in Fig. 3.

2.4. Collection of biological data

Biological data sampling was performed parallel to hydroacoustic data sampling during each survey with experimental (scientific), multi-panel gillnets equipped with a broad spectrum of mesh sizes and was complemented by sampling with large trawls having fine meshed cod-ends. All gillnets were made of mono-filament polyamid. Each setting comprises 7–9 nets (panels), usually with standard sets of eight nets with mesh sizes 18.5, 21, 26, 27, 28, 29, and 34 mm directed towards clupeoids mainly of the size groups covering the 2+-group (the RHS component in the Sound), as well as 55.0 mm directed towards gadoids. The panels were placed with a distance of 5 m between them. For further details on the gillnets see Poulsen et al. (2000) and Nielsen et al. (1998). Dependent on time, weather and water currents, fishing was stratified to cover bottom and pelagic water layers on both the Danish and Swedish side of the Sound within each geographical stratum. Both bottom and pelagic gillnet settings were carried out at localities where it was judged that there was highest probability of catching herring representatively according to fishermen experience and acoustic results. The total number of sets was 307. Complementary trawl sampling was performed at three stations in the northern, central and southern Sound area, respectively. Details of the fishing survey activities are presented in Table 1.

The gillnet catches do not fully represent species and size distributions occurring in the sea because of gear selection effects. For example, they do not cover the smallest size groups of herring or other species representatively. To compensate for this gear selection effect the estimated, normalised catches for all species and size groups, which were used to calculate abundance and length frequencies, were obtained by raising the gillnet catches by conversion factors calculated from selected data of overlapping trawl and gillnet catches. This is based on the assumption that the fine meshed trawl catches were representative for the species and size distributions occurring in the sea during that time and in that particular geographical stratum. All gillnet catches were multiplied (raised) with the specific conversion factors calculated for each geographical area, season of year, gillnet mesh size, species and fish size group. Details of the raising procedure are explained in Appendix A. By using the experimental gillnet fishing method from small research vessels it was possible to cover a wider geographical area (range of strata) and more depth strata including shallow water areas than was possible with the concurrent fine meshed trawl fishing operated from larger research vessels which have enough power to obtain a trawl speed which is sufficient for catching herring (clupeoids) of all size groups.

Catch in number and weight was determined for each fish species for each mesh size in all settings. The biological sampling included length measurements of all caught fish by species per mesh size, and total weight of catch by species per mesh size. More than 34 000 herring were caught. By-catch consisted mainly of whiting, cod, and garfish. Extended individual sampling of herring was performed in the southern, central, and northern part of the Sound, respectively, on selected fishing surveys covering all seasons of the year (e.g. on every second fishing survey). For each part of the Sound five herring specimens per half centimetre (semi-cm=scm) group were collected. Data on individual length, weight, and age (otoliths) were used. From the raised biological

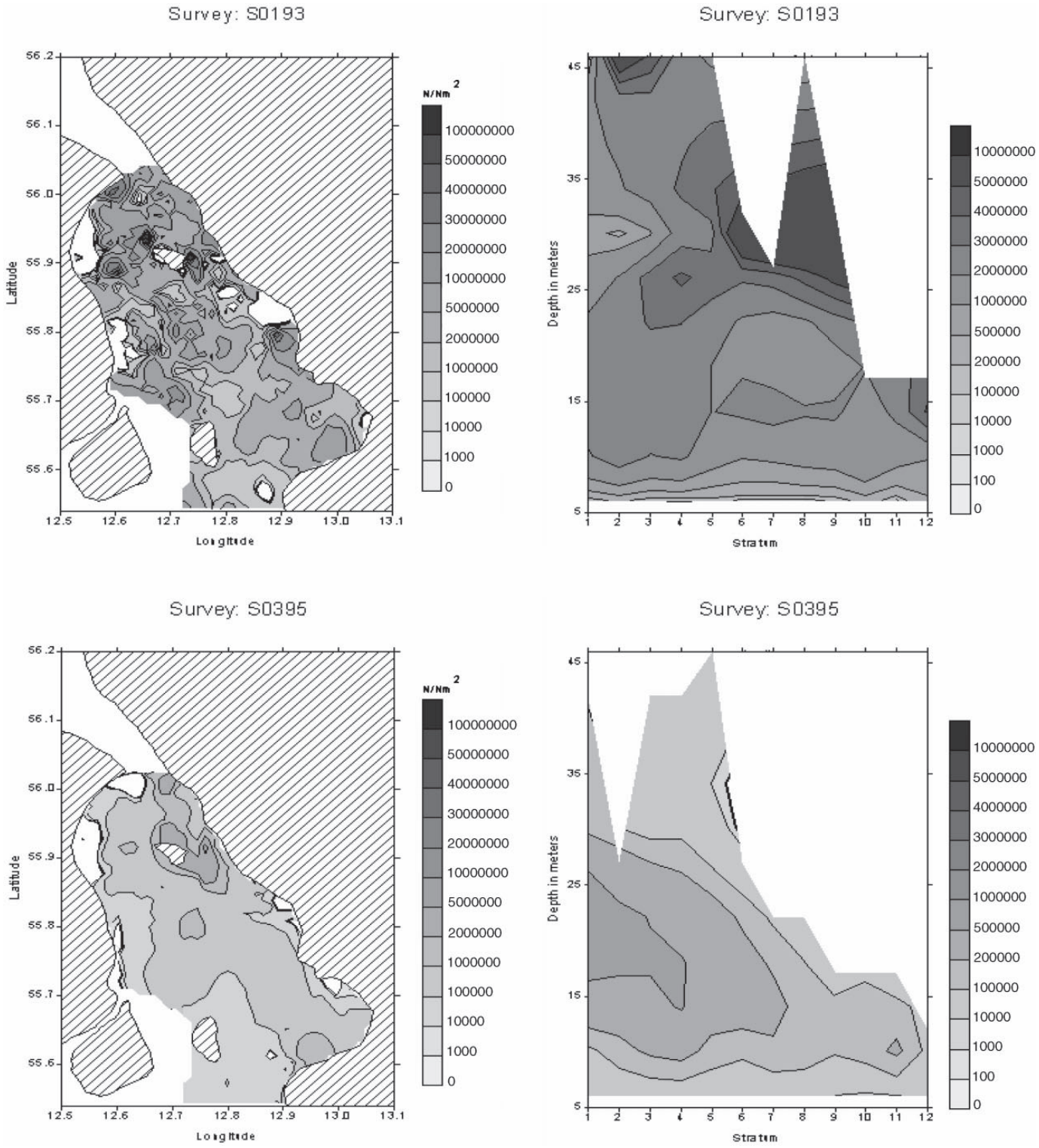

Fig. 3. Herring in the Sound in number per square nautical mile and per depth strata, respectively, in N/nm^2. Survey S0193 (September 1993, autumn) and S0395 (March 1995, spring). The contour plots are based on mean Sa values per geographical stratum and per depth stratum and are made using the kriging method.

data sampling species distribution and herring stock composition were analysed with respect to length (Fig. 4).

2.5. Collection of hydrographical CTD data

CTD data were collected with a SeaCat SBE19-03 or a Seabird SBE911+ on all surveys from October 1994 to May 1998 except May and October 1995 (see Table 1). Sampling comprised vertical profiles of pressure (db), temperature (°C), conductivity (μS/cm), oxygen probe current and temperature, UTC-time and date from about 0.5 m below sea surface down to as close to the bottom as possible. The data were processed with the Seasoft software package to produce corrected data of temperature, salinity and oxygen concentration versus depth. It was not possible to analyse oxygen samples from the SBE19-03. Consequently oxygen data from this Seacat relies on laboratory calibrations undertaken 2–3 times a year. This means that these data can be used only to indicate the order of magnitude change of the oxygen concentration with depth for each station. In each survey it was attempted to distribute 10–13 profiles evenly to represent all 13 geographical strata and all depth strata as well as to sample areas with high, intermediate, and low density of herring. Influence of the exact location of the haloclines and thermoclines on the vertical distribution pattern of the herring was determined (Fig. 5) by comparing features in the CTD-profiles at selected typical locations with profiles of acoustic integration values (S_a-values per 1 m depth strata) from the vicinity of these locations.

2.6. Collection of data on water currents

Data on water currents were collected (see Acknowledgements) with acoustic Doppler current profilers in the Sound at half hourly intervals at three different locations (Figs. 6 and 7). The Drogden profiler is located immediately south of the investigation area in the middle of the sill of the Baltic–Sound Kattegat estuary system. The Flinterenden and Ndr. Røse profilers are located just north of the southern border of the investigation area and cover the channels to the east and west of the island Saltholm (G10–G11, Fig. 1), respectively. Data from the survey period September 1993 to June 1998 were used, but the length of time series is different for the three locations. At each position currents were converted to components along and across selected directions and averaged over 6 h. From averaged time series cumulative flow along and across the selected direction was calculated for periods from July 1 in one year to June 30 in the next year. Main flow directions, 42°N at Drogden and Flinterenden and approximately 0° at Ndr. Røse, were selected because they give a near-zero cumulative cross flow component. Data from Ndr. Røse cover 17 half-meter layers from 1.6 m above the bottom up to surface for the whole period with only few short interruptions. Data from Flinterenden cover 16 half-meter layers of 0.5 m in the same depth range for a somewhat shorter period October 1993–December 1997 with few short interruptions and one long in April–June 1995. Data from Drogden cover depth intervals around 1.5, 2.8 and 4.1 m from July 1995 to June 1998 almost without interruptions. Only cumulative water flow along 0°N from Ndr. Røse, which has best coverage in time, is presented in Fig. 6, because scatter plots and linear regressions in Fig. 7 show a high degree of correlation between depth-averaged 6 h-average currents at different locations for time scales from 6 h and up. The cumulative flow was converted to kilometre of water passing the instrument since the start of each yearly period.

2.7. Comparison of estimated herring abundance with size of landings from fishery

Herring landings from the German commercial fishery at the spawning grounds (at Greifswalder Bodden) for the RHS in the spring period based on the official German catch statistics (O. Rechlin and T. Gröshler, pers. comm., Institut für Ostseefisherei (IOR), Rostock, Germany) are shown in Fig. 8.

2.8. Statistical analysis of herring density data

Herring density was analysed statistically and described by a GLM (Generalized Linear Model) ANOVA in relation to year, season of year, geographical division, depth stratum, temperature range and salinity range in order to test the hypotheses h:4–h:5. GLM procedure from the SAS statistical computer package version 6.12 (SAS, 1990, 1991b) was used to perform a parametric ANOVA on mean herring

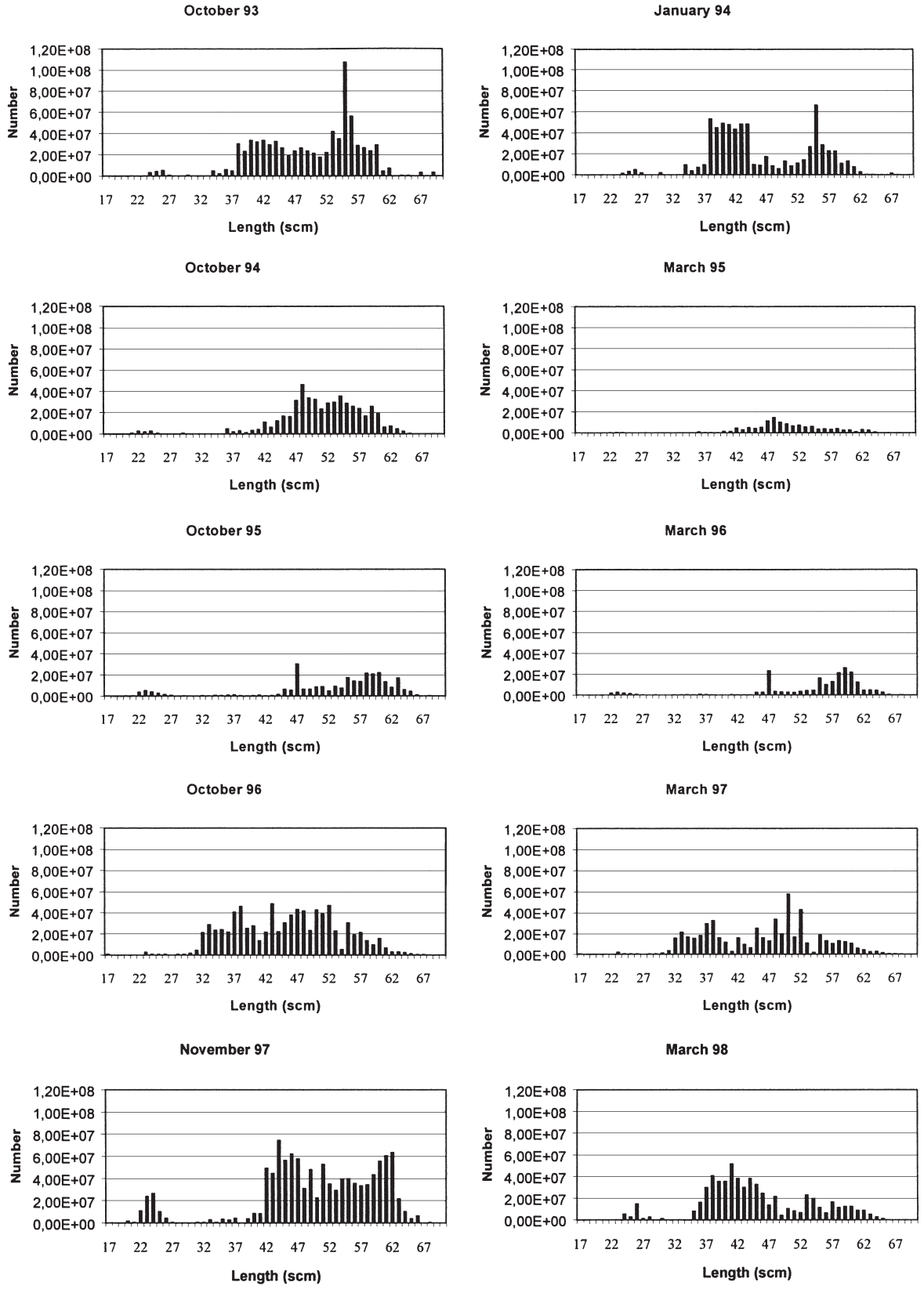

Fig. 4. Estimated length distribution of herring in the Sound in selected months in the spring and autumn seasons for each year in the survey period 1993–1998. The shown length frequencies are pooled data for all geographical strata (G01–G13). (January 1994 has been selected instead of February–March 1994 because not all of the survey area was covered in the two latter months.)

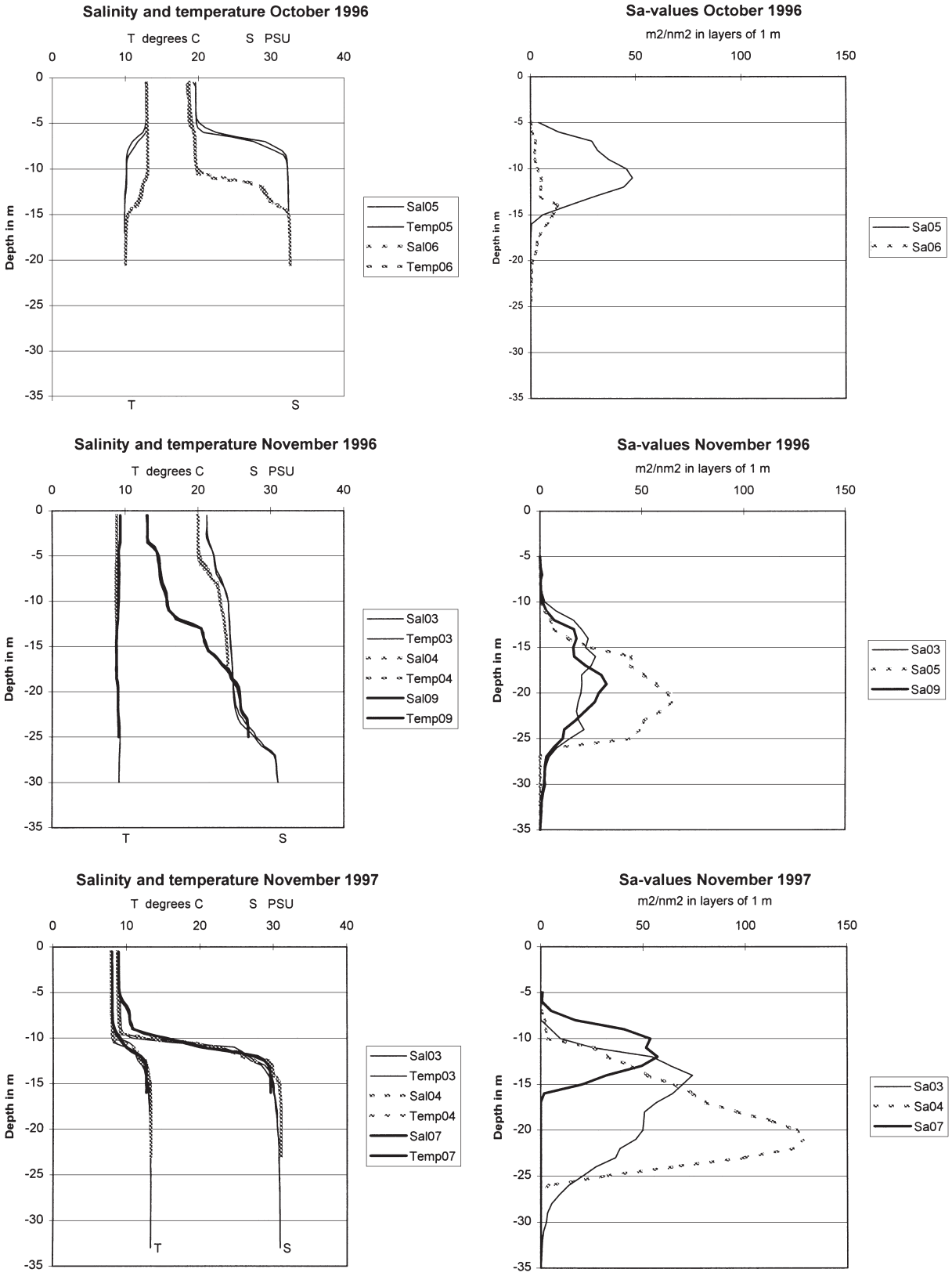

Fig. 5. Comparison between salinity–temperature profiles (CTD) and acoustic density profiles (Sa values) at selected positions in the area north of the island of Ven in the Sound. The profiles cover the water column from sea surface to sea bottom at the respective localities, except for the acoustic density profiles which do not cover the surface layer from 0 to 5 m depth.

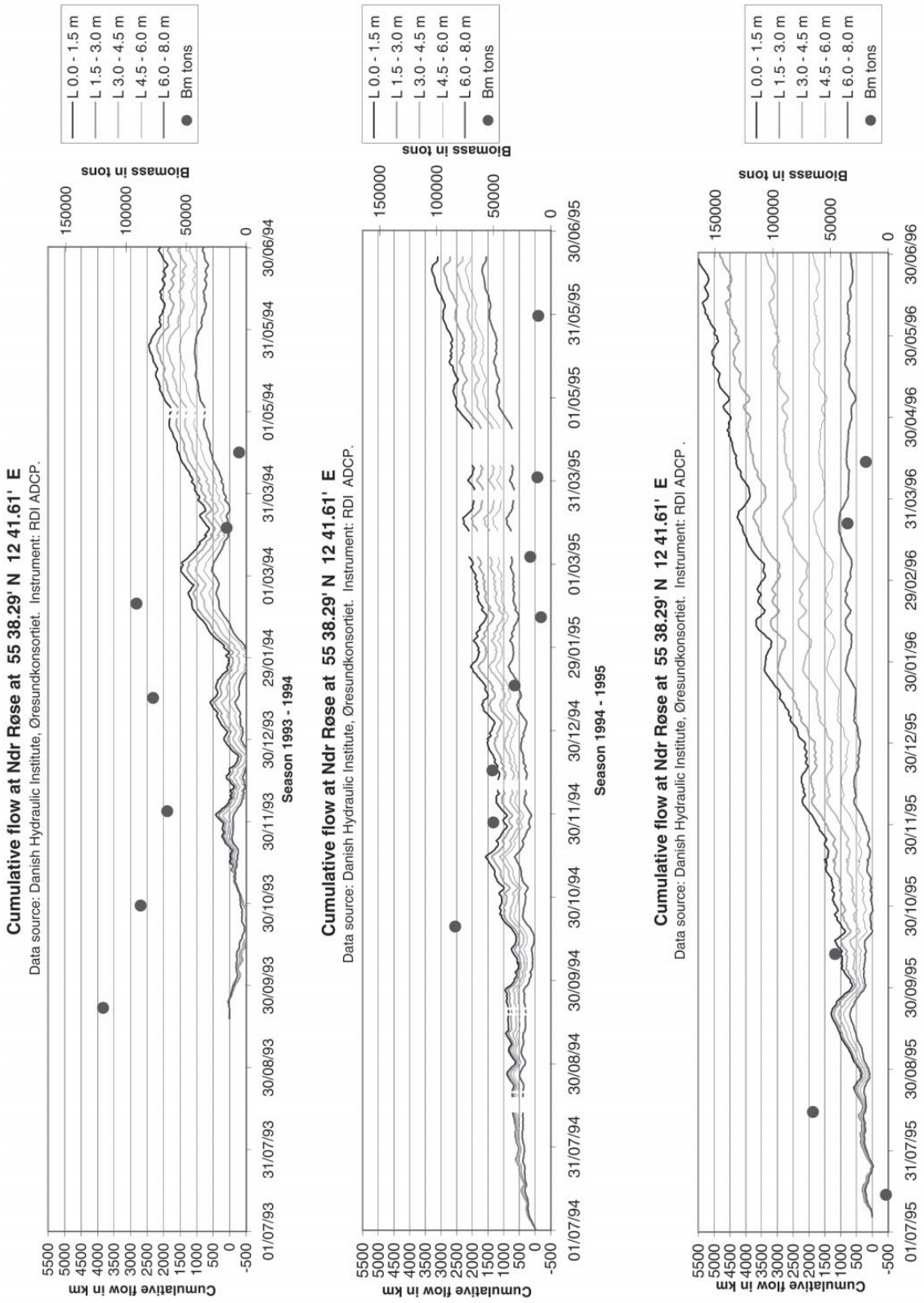

Fig. 6. Comparison between the herring biomass estimates (Bm) in tonnes and the cumulative water flow in kilometre past Nrd. Røse in different depth strata in the direction 0°N in the Sound. Uphill portions of the curves represent outflows from the Baltic and downhill portions inflows.

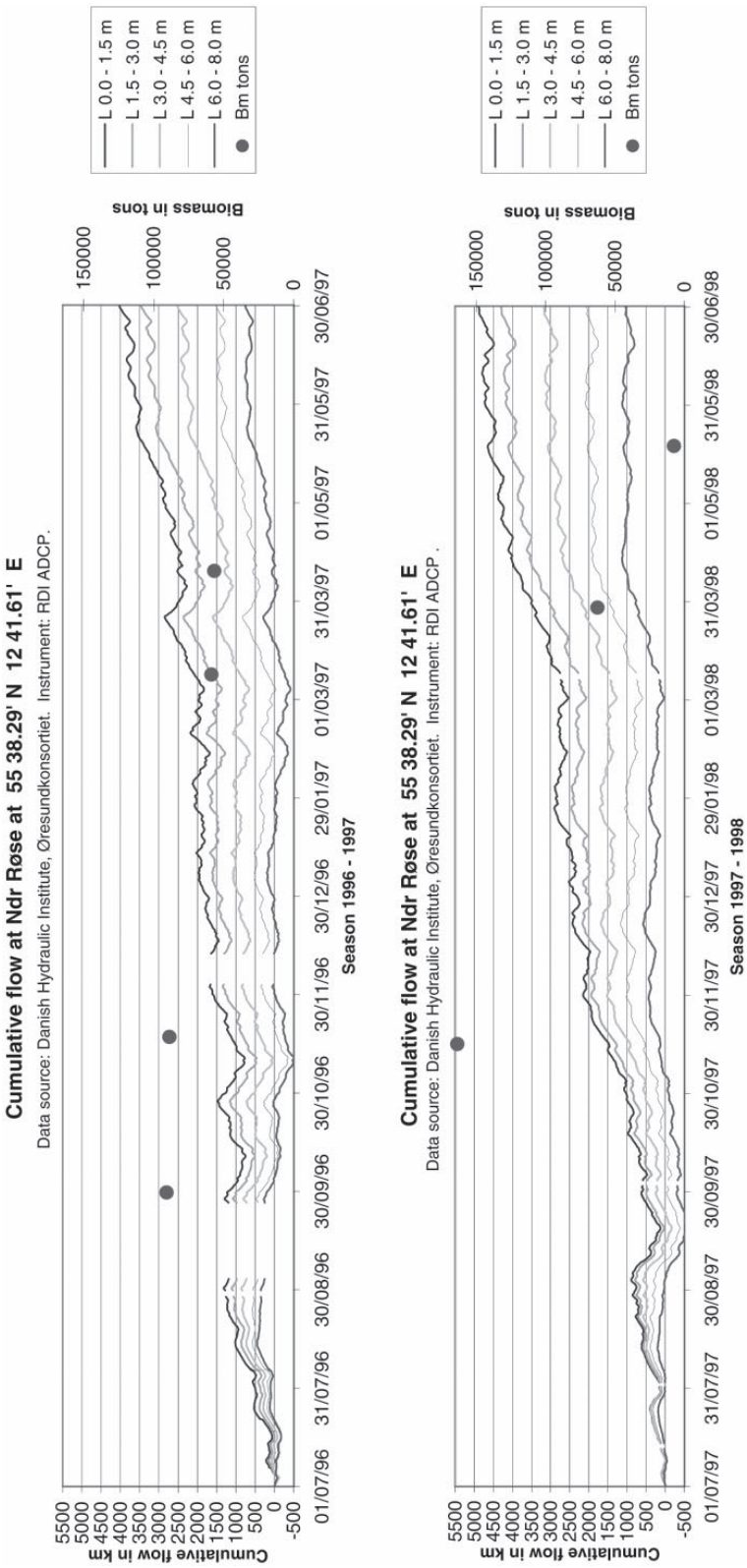

Fig. 6. (*Continued*).

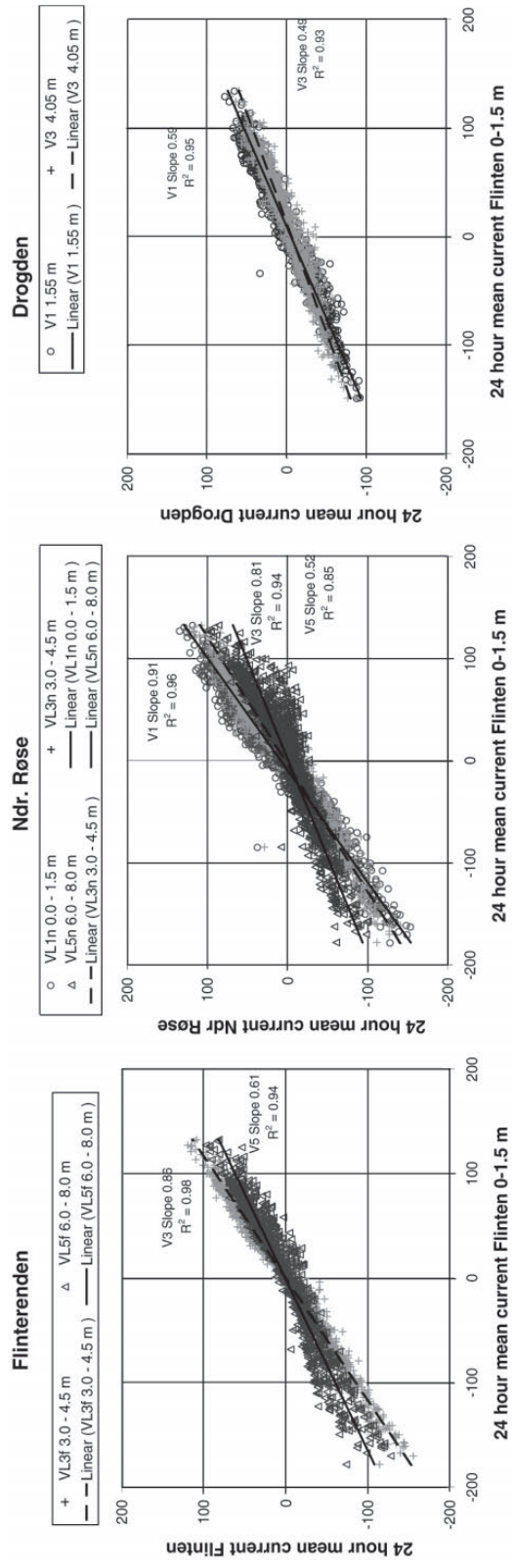

Fig. 7. Regression analysis of the correlation between the 24 h (~2×tidal cycles) mean of the near surface current at Flinterenden and the 24 h mean current at various depths at Flinterenden itself and at Nrd. Røse (both for the October 1993–December 1998 period), and at Drogden (July 1995–June 1998 period). The three different localities (Nrd. Røse, Flinterenden and Drogden) cover the Sound channels on both sides of the Island Saltholm.

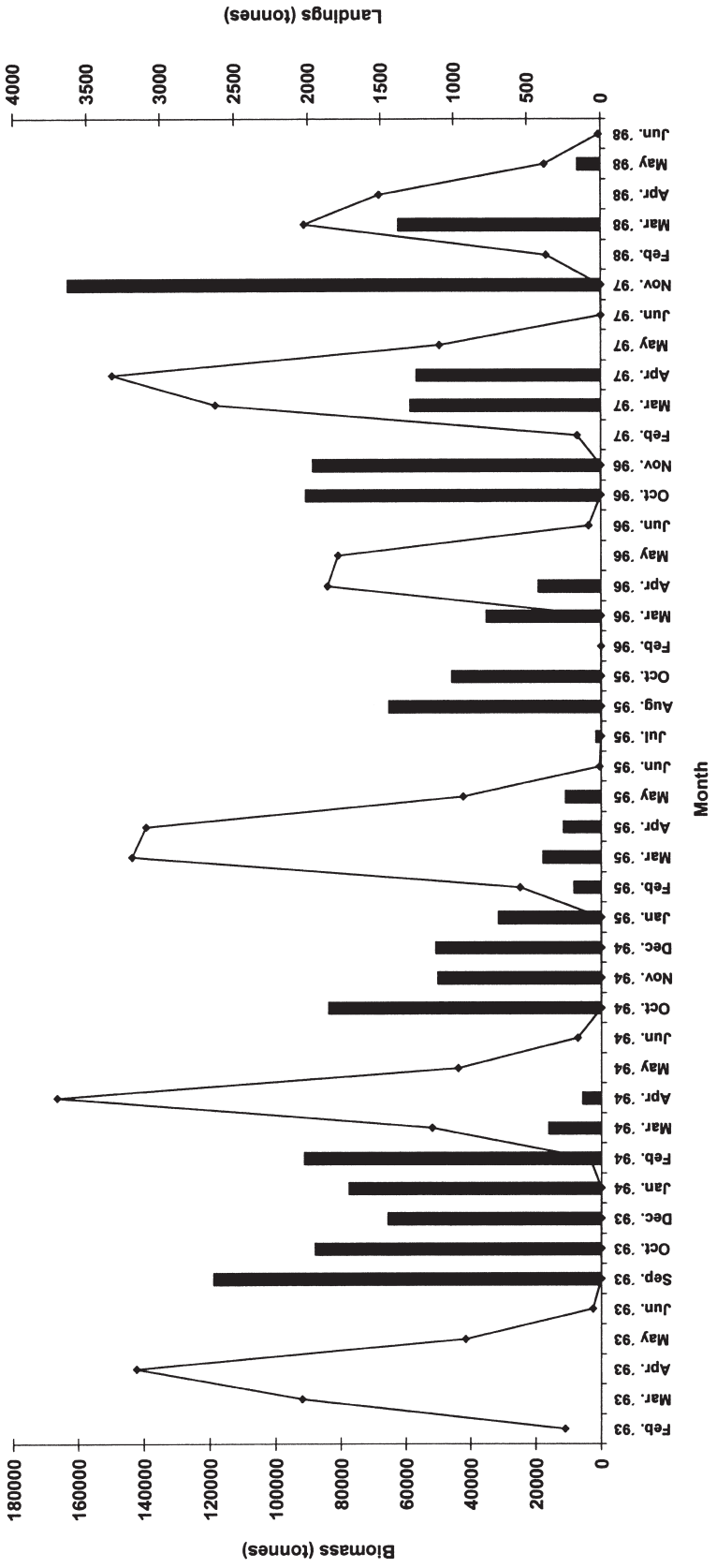

Fig. 8. The total biomass (tons) in the Sound (bars) and German landings (tons) (solid lines) from commercial fishery at the spawning site at Griefswalder Bodden.

density (dependent variable) by changing the multiplicative model

$$N/\mathrm{nm}^2_{Y,\mathrm{SY},\mathrm{GS},\mathrm{DS},\Delta S,\Delta T} = Y_Y \times \mathrm{SY}_{\mathrm{SY}} \times \mathrm{GS}_{\mathrm{GS}} \times \mathrm{DS}_{\mathrm{DS}} \times \Delta S_{\Delta S} \times \Delta T_{\Delta T} \times \varepsilon_{Y,\mathrm{SY},\mathrm{GS},\mathrm{DS},\Delta S,\Delta T}$$

to the linear (additive) model (by logarithmic transformation of CPUE-data)

$$\ln(N/\mathrm{nm}^2_{Y,\mathrm{SY},\mathrm{GS},\mathrm{DS},\Delta S,\Delta T}) = Y_Y + \mathrm{SY}_{\mathrm{SY}} + \mathrm{GS}_{\mathrm{GS}} + \mathrm{DS}_{\mathrm{DS}} + \Delta S_{\Delta S} + \Delta T_{\Delta T} + \ln(\varepsilon_{Y,\mathrm{SY},\mathrm{GS},\mathrm{DS},\Delta S,\Delta T})$$

where Y is the year (1993–1998); SY the season of year (autumn, spring); GS the geographical stratum (G01–G13); DS the depth stratum 6: 5–7.5 m, 16: 7.5–22.5 m, 26: 22.5–32.5 m and 46: >32.5 m; ΔS (delta S) the salinity range, numerical difference between minimum salinity and maximum salinity in order to investigate the effect of the location of the halocline (ranges: $\Delta S<2.0 \Rightarrow \Delta S=1$; $2.0 \leq \Delta S<10.0 \Rightarrow \Delta S=2$; $10.0 \leq \Delta S<20.0 \Rightarrow \Delta S=3$; $20.0 \geq \Delta S \Rightarrow \Delta S=4$); ΔT (delta T) the temperature range, numerical difference between minimum temperature and maximum temperature in order to investigate the effect of the location of the thermocline (ranges: $\Delta T<2.0 \Rightarrow \Delta T=1$; $2.0 \leq \Delta T<10.0 \Rightarrow \Delta T=2$; $10.0 \geq \Delta T \Rightarrow \Delta T=3$); ε (epsilon) model error term (model residuals).

The GLM ANOVA was used as this procedure can handle unbalanced data, i.e. where the number of observations vary by cells. First the additive model was tested including all first-order interactions effects (Model 1 in Table 2) in order to identify all statistical significant interaction effects. Then followed a test of the additive model including only main effects (Model 2 in Table 2) to obtain model estimates of the statistically significant main effects. The resulting reduced models were achieved by successive reduction of non-significant effects (5% level). In the run of the first model no main effect was removed if the effect was included in a significant interaction effect. The test statistics and the estimates of the ANOVA for each reduced model are presented in Table 2. The residuals of the models were analysed by the SAS Univariate procedure (SAS, 1991a,b) as a test of the errors being normally distributed and having equal variances. The tests show that the data were valid and that models 1 and 2 describe the density data well on the 1% level with 71 and 58% of the total variation accounted for, respectively, in the density data.

3. Results

The most abundant species by far in the Sound is herring. Abundances of 45–165 000 t in August–February, 5–60 000 t in March–May, and <2000 t in June–July were found with peak abundance in the autumn (Table 1). This indicates a longer over-wintering period from August to March than hitherto assumed from September/November to December/January which leads to rejection of hypothesis h:1. The herring biomass of 165 000 t measured in autumn 1997 corresponds to approximately 1.125×10^9 herring (Table 1). The biomass of herring in the Sound was relatively small in 1995–1996 compared to the rest of the period 1993–1998. The present biomass estimates of herring (2+-group) in the Sound compared with estimated size of spawning stock biomass (3+-group) for RHS as well as with international landings of spring spawning herring in the western Baltic Sea and Skagerrak–Kattegat (Tables 1 and 3, Fig. 8) indicate that the Sound is an important over-wintering and/or migration area for RHS. This leads to acceptance of hypothesis h:2. Local, annually resident and spawning herring stock components in the Sound does not contribute important biomass because the total herring biomass decreases to around 5000 t or less during summer (May–July) (Table 1, Fig. 8). This low biomass during summer and the following periods with high biomass indicate that the main component of herring in the Sound is RHS which leads to acceptance of hypothesis h:3.

Observed herring abundance decreases in the Sound during spring are generally in good agreement with the timing of (subsequent) peak landings in the German herring fishery at the spawning grounds (Griefswalder Bodden and surrounding areas) for RHS (Fig. 8, Table 1). In 1994, 1995, 1997 and 1998 declines in abundance were observed in February–March or January–February and the corresponding fishery at the spawning grounds reached its maximum a little later in March–April (Fig. 8). In spring 1996, there was a delayed decline in herring abundance in the Sound until March–April, and the corresponding fishery did

Table 2
The descriptive statistics of the GLM analyses of variance and estimated parameters from the additive GLM models as well as estimates of the different main effects from Model 2. The sum of squared deviations (s. of sq.) for the various dependent effects are of type III sum of squares for the models (SAS, 1990, 1991a,b), which for type III is independent of the order of the effects in the model. Finally, descriptive statistics of the test of normality for each model is shown

Source	Model	Degrees of freedom	Sum of squares	F	Probability>F
Descriptive statistics					
Model	1	125	2440.7	15.4	0.0001
Error	1	786	996.5		
Corrected total	1	911	3437.1		
R^2	1				r^2=0.71
Model	2	26	1984.3	46.49	0.0001
Error	2	885	1452.9		
Corrected total	2	911	3437.1		
R^2					r^2=0.58
Year	1	5	160.42	25.31	0.0001
Season of year	1	1	82.23	64.86	0.0001
Geographical stratum	1	12	256.43	16.86	0.0001
Depth stratum	1	3	583.44	153.40	0.0001
Year×season of year	1	3	28.12	7.39	0.0001
Year×geographical stratum	1	55	132.44	1.90	0.0001
Year×depth stratum	1	15	95.97	5.05	0.0001
Season of year×depth stratum	1	3	53.83	14.15	0.0001
Geographical stratum×depth stratum	1	28	122.69	3.46	0.0001
Year	2	5	267.76	32.57	0.0001
Season of year	2	1	88.26	53.68	0.0001
Geographical stratum	2	12	368.89	18.70	0.0001
Depth stratum	2	3	793.06	160.77	0.0001
Salinity range	2	3	21.08	4.27	0.0053

Parameter	Model	Group	Estimate	T for H0; Par.=0	Probability>|T|
Logarithmic transformed estimates of parameters from main effect model (*Model* 2)					
Intercept	2	Intercept	6.86	12.36	0.0001
Year	2	1993	1.02	4.46	0.0001
	2	1994	0.22	1.14	0.2552
	2	1995	−0.85	−4.73	0.0001
	2	1996	−0.41	−2.04	0.0413
	2	1997	−0.12	−0.59	0.5572
	2	1998	0		
Season of year	2	Autumn	0.73	7.33	0.0001
	2	Spring	0		
Geographical stratum	2	G01	2.69	5.89	0.0001
	2	G02	2.37	5.20	0.0001
	2	G03	2.38	5.25	0.0001
	2	G04	2.25	4.98	0.0001
	2	G05	2.05	4.53	0.0001
	2	G06	1.88	4.14	0.0001
	2	G07	1.07	2.34	0.0195
	2	G08	1.57	3.37	0.0008
	2	G09	1.48	3.18	0.0015
	2	G10	1.32	2.82	0.0049
	2	G11	0.87	1.86	0.0638
	2	G12	−0.03	−0.07	0.9409

Table 2 (*Continued*)

Parameter	Model	Group	Estimate	*T* for H0; Par.=0	Probability>|*T*|
	2	G13	0		
Depth stratum	2	6	−0.90	−5.84	0.0001
	2	16	1.35	8.39	0.0001
	2	26	0.79	4.96	0.0001
	2	46	0		
Salinity range (ΔS)	2	1	−0.61	−2.24	0.0251
	2	2	−0.18	−0.63	0.5280
	2	3	−0.10	−0.31	0.7589
	2	4	0		
Variable		*N*	*W*:normal	Probability<*W*	
Test of normality					
Residuals	1	912	0.98	0.05	
	2	912	0.99	0.86	

first peak in April–May. The levels of relative decrease in herring biomass from autumn 1997 to spring 1998 were similar to decreases in spring 1994–1996 from the previous autumn periods. However, in spring 1997 there was an even more pronounced delay in biomass decline than in spring 1996. In spring 1998 the fishery was different from the typical situation as landings declined from normal quantities in February–March to a relatively lower level in April compared to other years. Afterwards, fishing stopped mainly because of low herring abundance's at the spawning grounds. From estimated length distributions in March 1998 (Fig. 4) it appears that a large amount of smaller herring was still present in the Sound. The general correspondence between estimated herring abundance in the Sound and subsequent peak landings in herring fishery at the RHS spawning places also support acceptance of hypotheses h:2–h:3 and rejection of hypothesis h:1.

Table 3
Present biomass estimate of the 2+-group (in tons) in the Sound in the autumn and the ICES estimate of spawning stock biomass (SSB) (3+-group) as well as the official international landings of spring spawning herring in the western Baltic Sea, Skagerrak–Kattegat and the North Sea. (sources: ICES, 1998, 1999)

Year	Biomass Sound (t)	ICES SSB (t)	Landings (t)
1993	118.000	Not good quality	171.000
1994	84.000	Not good quality	163.000
1995	65.000	Not good quality	174.000
1996	91.000	162.000	132.000
1997	163.000	205.000	106.000

Abundance was relatively high in autumn 1993 and in the autumns 1996–1997 (Table 1, Fig. 8), corresponding to the strong 1988 and 1991 year classes (Fig. 4). The 1988 year class was observed in autumn 1993 as the five w-ring-group with mean length of around 55 scm (Fig. 4). The 1991 year class was observed as the two w-ring-group in autumn 1993 with mean length around 41–42 scm and again in autumn 1994 as the three w-ring-group with mean length around 48 scm, whereas the 1988 year class as six w-ring-group had declined in autumn 1994 (Fig. 4). In autumn 1996 (Fig. 4) the two w-ring-group, i.e. the 1994 year class, with length around 37–42 scm, represents a much larger part of the herring abundance compared to 2-group abundance in the autumns of the two previous years, 1994 and 1995. This strong 1994 year class can again be identified in autumn 1997 as the three w-ring-group with mean length around 45 scm where it remains an important component of the biomass. (Figs. 4 and 8, Tables 1 and 2). In general, strong year classes were first observed in the Sound as two w-ring-group fish during autumn (Fig. 4). The strong year classes in the Sound (1988, 1991 and 1994) are in good agreement with strong year classes for the RHS stock based on larval index for the stock

Table 4
Yearly estimates of larval indices for 0-group RHS (TL≥30 mm) at the spawning sites during March/April–June (ICES, 1999)

Year	Larvae number in millions
1986	1500
1987	1370
1988	1223
1989	63
1990	57
1991	236
1992	18
1993	199
1994	788
1995	171
1996	31
1997	54
1998	2202

(ICES, 1999) estimated from larvae surveys at the spawning grounds in Griefswalder Bodden and adjacent waters in late spring (Table 4). Even though larval index merely is an index of total spawning stock and does not give an exact estimate of year class strength because of unknown natural mortality before recruitment it does indicate a potential for a coming good year class (Table 4). These larvae investigations are further described in Biester (1989), Scabell and Jönsson (1989) and Müller and Klenz (1994). High larval indices have been monitored only in 1991, 1994 and 1998 since 1988 (Table 4). The agreement in observations of strong year classes and first observation of these as 2-group fish also suggest validity of hypotheses h:2–h:3.

The largest herring size groups seem to migrate southwards towards the spawning grounds in spring before the smaller ones (Fig. 4). During autumn/winter a relative higher proportion of herring in the Sound belongs to the large size groups (older herring) compared to the proportion of large herring in spring (Fig. 4). This is in agreement with age distributions observed in the German commercial fishery at the spawning grounds directed towards the RHS. In this fishery 5+ w-ring-group herring is typically dominant in catches in the beginning of the season, March, whereas the four and three w-ring-groups become dominant in April and May. (O. Rechlin and T. Gröshler, pers. comm., IOR, Rostock, Germany). This leads to acceptance of hypothesis h:7.

The results of herring density analysis by GLM ANOVA are given in Table 2 and typical density patterns during autumn and spring are shown in Fig. 3. In general, densities were highest in the northern strata around the island of Ven and in autumn (Tables 1 and 2, Fig. 3). Furthermore, densities were highest in the depth stratum 7.5–22.5 m from sea surface followed by depth stratum 22.5–32.5 m, while density always was relatively low in the surface layer 5–7.5 m (Fig. 3, Table 2). Densities increased with increasing salinity range, and were highest where the salinity range was highest, i.e. in the layers where the pycnocline was located (Fig. 5, Table 2). Where the water was stratified peak densities of herring occurred typically just below (or in) the halocline. There were no concentrations of herring in the southern Sound close to the Drogden threshold during spring before the southwards spawning migration, and highest densities in this period were observed in the northern strata and in the deeper parts (Fig. 3). The thermocline does not seem to influence herring densities (Table 2). The above observations lead us to accept hypothesis h:4 and reject hypothesis h:5.

3.1. Water flow past Drogden versus estimated herring biomass

Average total outflow from the Baltic through the Sound and Belt Sea is about 450 km^3 a year mostly due to river runoff to the Baltic Sea area (Jacobsen, 1980). About one third of this passes the Sound causing generally outgoing brackish currents in the surface layers and generally ingoing saltier compensation currents below the halocline driven by mixing processes in the halocline layer. Overlaying these flows there is a strong pattern of inflow and outflow caused by atmospheric conditions (wind and pressure) over the Skagerrak–Kattegat–Baltic area. Also there are relatively weak tidal currents, about 20 cm/s pp (peak to peak) at neap tide and 60 cm/s pp at spring tide at Flinterenden and less at other locations compared to variations of 200–300 cm/s in atmospherically driven flows.

To test hypothesis h:6 that herring might take advantage of or be triggered by strong inflow situations during southbound springtime migration, estimated total herring biomass is plotted in Fig. 6 together with cumulative flow data. Indications of

such behaviour, that is, distinct decrease in herring biomass in the Sound in combination with significant inflow to the Baltic between two surveys, was observed on some occasions (Fig. 6), for example in February–March 1994, in January–February 1995, and in March 1996. Also there is indication of a delayed migration in spring 1998, due to an extended outflow period in March–April 1998. This suggests acceptance of hypothesis h:6, however there are very few biomass estimates (surveys) during the later years to make a conclusive test of the hypothesis. There is also opposing evidence, for example in March–April 1997, when there is little or no change in the measured herring biomass, in spite of a notable inflow period.

4. Discussion

The present investigations are the first to give quantitative estimates of the occurrence of RHS in the central Sound over the year during a several year period as well to analyse herring distribution and density patterns here in detail, and investigate the possible influence of hydrographical factors on distribution and migration.

Highly variable environmental factors influence RHS as it lives in transitional areas between the Baltic and the North Sea, which are mixing areas for several herring stocks and, furthermore, RHS is often exposed to heavy exploitation here (Biester, 1979a,b; ICES, 1983a, 1998; Otterlind, 1984, 1987). The state of the stock is uncertain due to problems with defining the proportion of spring and autumn spawners using historical data and due to lack of co-ordinated comprehensive surveying on RHS (ICES, 1999). The full stock has never been covered by ICES international hydroacoustic surveys for stock assessment purposes in all of its distribution area (ICES, 1994a,b, 1998). Furthermore, historical catch at age data used in stock evaluation — and consequently historical biomass estimates — are also uncertain due to low sampling intensity which, however, has improved in later years (ICES, 1999). However, the spawning stock biomass was at relatively high level up to around 1990 (probably between $\frac{1}{2}$ and 1 million tons) because of constant high yearly recruitment to the spawning stock up to around 1990 (ICES, 1999) while the year class strength has varied considerably since 1988 with only a few strong year classes. A new method to split autumn and spring spawners in the evaluation of herring stocks in the western Baltic Sea and Skagerrak–Kattegat has suggested a considerable number of autumn spawners in catches of older age classes (ICES, 1999).

The shown patterns in herring occurrence and distribution based on quantitative measurements agree with some of the results from qualitative and anecdotal studies from literature. Recoveries from comprehensive herring tagging experiments (Biester, 1979a,b; Jönsson and Biester, 1981; Aro, 1989) indicate that the Sound is an important migration route for RHS. However, the present results indicate longer overwintering in the Sound than previously believed. Otterlind (1984, 1987) suggests that RHS mainly stay with high abundance in the Sound from September–November to December–January, while the present results show high abundance in a more prolonged period from August to March. This is a somewhat different timing in migration of RHS from what traditionally believed. Biester (1979a,b) suggests that probably more than 75% of herring in the Sound in autumn–winter are RHS, and that recoveries from the 1950s and 1970s are practically the same, indicating stability in the stock migration pattern. Otterlind (1984, 1987) and ICES (1983a, 1998) also suggest over-wintering RHS to be the dominant herring component in the Sound during autumn–winter which mainly comprise mature herring (2+-groups). Historically, several local stocks have been identified in the Sound (Jensen, 1957; Otterlind, 1987), among those one that spawns during January–March along the Höganäs-Kullen coast with distribution into the northern Sound (Otterlind, 1984, 1987). However, these local stocks have been only historically abundant. No significant local spawning has been found since around 1980, nor any local, more or less permanent populations, or any evident spawning grounds from Helsingør-Helsingborg to Dragør-Malmö recently.

Strong year classes were first observed in the Sound as two w-ring-group during autumn in the present study. This agrees with previous reports of age specific migration of RHS. Mature herring have been reported to participate in early northwards summer feeding migration up into Kattegat–Skagerrak just after spawning. Migration patterns for those two w-ringers that spawn (mature) in spring and those who do not

spawn (immature) is somewhat different. Only larger specimens and first-spawners (post-spawners) of the two w-ring-group take part in this north-westwards migration after late spawning (May–June) whereas the three w-ring-group, which spawns earlier, all participate. (Biester, 1979a,b; Jönsson and Biester, 1979, 1981; ICES, 1983a, 1998; Otterlind, 1984, 1987; O. Rechlin, pers. comm., IOR, Rostock, Germany). Some young herring migrate eastwards from the spawning grounds to the border waters of the Bornholm basin, while some stay in the south-western Baltic Sea during winter. In autumn the one w-ringers are not an important part of the total herring biomass in the Sound. This is supported by literature (Otterlind, 1984, 1987) as well as by results on age distributions from acoustic surveys (survey reports from the R/V Solea ICES international acoustic survey in the western Baltic Sea in autumn, 1993–1998, O. Rechlin, pers. comm., IOR, Rostock, Germany). That migration of two w-ring herring is only partly associated with that of older RHS is also shown by studies on parasite infestations with *Anisakis* (Nematoda) larvae which are used as biological tags for RHS (ICES, 1983a; Kühlmorgen-Hille, 1983). It was found that the degree of infestation increases with age and that juveniles and some recruit spawners (zero-, one- and partly two-ringers) usually lack parasites. This agrees with the observation that early hosts for the *Anisakis* larvae are Euphausiid species which are absent in the very brackish Baltic waters.

The observed months with peak biomass of herring in the Sound; the concordant or following peaks in landings from German fishery at the spawning grounds; the subsequent peak larval indices at the spawning grounds; the observed strong year classes in the Sound, the corresponding potential for corresponding strong year classes found in larval indices from the spawning grounds; the size (age) dependent southwards spawning migration pattern, the corresponding age distributions in German fishery at the spawning grounds (where early catches typically are dominated by the larger herring); as well as the above described distribution of the two w-ring herring; are in combination a strong indication that main herring component in the Sound is RHS and that the Sound is possibly the major over-wintering area for RHS.

Herring were found to stay mainly in deeper, northern parts of the Sound in or below the halocline in stratified waters during autumn, winter and spring. Thus, no concentrations were found in the southern Sound in spring before the southwards migration. The mainly northern distribution in autumn–winter is supported by literature studies of historical fisheries (Otterlind, 1984, 1987). Since the herring tend to stay in or below the halocline, they might during southbound migration take advantage of strong inflow events when high saline water comes to the surface, by migrating with the current direction and so save energy. Rapid decreases in biomass could indicate such situations. Alternatively, delays in migration might be expected during periods of extended strong outflow that could result in constant or slightly increasing biomass during such occasions. Indications of such behaviour can be observed at some occasions in the results. However, in most periods between two subsequent surveys there are observed situations with both inflows and outflows which complicates conclusions on the matter. With regard to north-westward migration after spawning only relatively few spent herring were found in the Sound, and no distinct and consequent temporal, geographical and sex specific patterns in distribution could be distinguished for spent herring (Nielsen, 1996; Nielsen et al., 1998). However, sexual maturity indices suggest that spent herring do not concentrate in the Sound and that there is some continuous migration in spring from March to May of spawned herring through the Sound.

To clarify the distribution and migration patterns of RHS and factors affecting it, and to obtain good quality stock estimates, surveys are necessary at least once a year, covering the full stock distribution area. Further repeated and overlapping monitoring over the year (during several years) in the Sound and the Belt Sea is necessary to quantify the relative importance of the two migration routes for RHS. Exchange between the central Sound and the Kattegat and Køge Bay should also be investigated. Further tagging experiments and maturity studies are also necessary to map completely the north-westwards migration of the spawning stock from spawning to feeding areas, and investigations on feeding during the prolonged over-wintering period in the Sound are relevant. More stock affiliation studies of herring in this whole transition area are needed to distinguish between different stock components, e.g. by use of micro-satellites or otolith micro-structure characteristics.

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Appendix A.

A.1. Procedure for raising of gillnet catches to estimated species and length distributions in the population

The collection of both fishery and hydroacoustic data is based on the principle of random stratified sampling and the sampling of the two types of data are generally overlapping in time and space. As the gillnet catches do not fully represent species and size distributions occurring in the sea because of gear selection effects, the estimated, normalised catch for all species and size groups, which were used to calculate abundance and length frequencies and evaluate hydroacoustic data, was obtained by raising gillnet catches. This was done by calculating conversion factors between catch numbers for trawl and gillnet per fish species and fish length group and per gillnet mesh size for selected hauls/sets which were overlapping in time and space, i.e. for each geographical area (stratum) and season. Then the catches of all (other) gillnet sets within the same area and within that autumn and the following spring period for each separate year were accordingly multiplied by the specific conversion factors (raised) for each geographical area, season of year, gillnet mesh size, and species and fish length group. Accordingly, all gillnet surveys were raised by the obtained correction factors. This was done under the assumption that the fine meshed trawl catches were representative for the species and size distributions occurring in the sea during that time and in that particular geographical stratum. This method ensure that differences between different gillnet catches is kept by just multiplying with a factor for all of them.

Each autumn (October) 1993–1998 the ICES international Baltic hydroacoustic survey with R/V Solea covering the western Baltic Sea (ICES Subdivision 22–24) was performed covering 3–4 trawl stations in the central Sound (ICES Subdivision 23). Trawling was performed with large Octopus-trawl in 1995–1997 which is modified from the large ‘‘Blacksprutte’’-trawl used in 1993–1995 both having small meshed cod-ends (ICES, 1998). The trawl fishery covered the whole water column at the trawl stations. Trawl stations and gillnet fishery stations which were overlapping in time and space (within the same geographical stratum) were selected both for the northern part of the Sound covering the geographical strata G01–G05 as well as for the southern part covering the geographical strata G06–G13 (Fig. 1). For these overlapping stations the gillnet catches were raised according to the method described above. This was done for the most important pelagic and semi-pelagic species in the Sound (herring, cod, whiting (*Merlangius merlangus*), and sprat (*Sprattus sprattus*)). Trawl catches standardised to half an hour fishery were used in the raising. By using the described raising method the specific species and size distributions found for each geographical stratum and each month (survey) were incorporated from the gillnet catches and raised by a correction factor to be used in the biomass estimation and in analysis of herring size distribution based on the comprehensive coverage in time and space of the gillnet catches. Because of insufficient gillnet catches in July 1995 (S0695) and in the spring

1998 (S0398 and S0598) trawl catches (with small meshed cod-end) concurrent with the hydroacoustic echo integration were used directly in order to calculate species and size distributions to be assigned to the acoustic energy data (Sa-values) here. These trawlings covered both the northern and southern part of the Sound. During the May 1995 acoustic survey (S0595) no concurrent biological sampling was performed but data from April 1995 was used to evaluate the hydroacoustic data.

A.2. Procedure for estimating fish abundance from combined acoustic and fishery data

For each stratum acoustic mean target strength (TS) was estimated for the most important fish species in the Sound (herring, whiting, cod, sprat) using the empirical standard TS algorithms (ICES, 1992): clupeoids (ICES, 1983b) and gadoids (ICES, 1984)

$$\text{Clupeoids}: \quad \text{TS} = 20\log_{10} L - 71.2$$

$$\text{Gadoids}: \quad \text{TS} = 20\log_{10} L - 67.5$$

The two echo sounder systems (see materials and methods) were connected to an EchoAnn data collection and analysis unit. Settings of the two sounders were high power, 1 ms pulse duration, 3 kHz/1 kHz receiver bandwidth, SL+VR 109.9 dB/132.5 dB, $10\log\psi$ −12.9 dB/−20.2 dB, sound velocity 1470 ms^{-1}/1472 ms^{-1}, pulse length 1 ms, TVG constant 64.6 dB/64.6 dB, respectively, for the EY200/EK400 systems. The SL+VR values were obtained by calibrating the sounders against a standard copper sphere target of 60 mm (Foote et al., 1986; Degnbol, 1988; Degnbol et al., 1990). Uncertainty of the calibration factor was found to be approximately 1 dB corresponding to ±12% for the EY200 system and approximately 0.5 dB (±5%) for the EK400 system.

An overall mean TS for each geographical stratum was estimated according to species and size distributions (in weighted proportions of occurrence of species and length groups in the raised catch) from the biological samplings divided into stratum. The following equations of values for TS and Sa are expressed in a linear form instead of in a logarithmic form. The mean area back scattering strength (Sa) for each geographical stratum as well as the total number of fish (scatters) for each stratum were estimated as

$$\overline{\text{Sa}}\ \ (\text{stratum}) = \sum_{i=1}^{j} \frac{\text{Sa}_j}{j},$$

j = number of logs per geographical stratum

$$N = \left(\frac{\text{mean Sa}}{\text{mean TS}}\right)\ \text{stratum area}$$

Allocation to length group for each species was assumed to be in accordance with the length distribution for each species in the raised catch. Sa-values were calculated for each log, where one log represents 6 min of hydroacoustic sampling which corresponds to a distance of around 0.5 nautical mile when sailing with a speed of approximately 5 kn. Sa is calculated for each log by summing the Sa values for all pings within the log and then dividing by the total number of pings within the log. Species and size distributions and mean TS calculations on geographical stratum level is then assigned to all the log-based Sa-values located within a given geographical stratum. The density of fish per log per species given in number of fish per square nautical mile is then calculated as

$$N/\text{nm}^2 = \frac{\text{Sa}_{\text{log}}}{\text{mean TS}_{\text{stratum}}}\text{species fraction}_{\text{stratum}}$$

Species and size composition is assumed to be identical for all depth strata within a given geographical stratum and, consequently, the same mean TS for all depth strata in the geographical stratum is used here. The total number of fish per stratum and depth stratum is calculated as follows, which of the following can be split into species using the species fraction per stratum

$$N_{\text{stratum,depth stratum}} = \frac{\text{mean Sa}_{\text{stratum,depth stratum}}}{\text{mean TS}_{\text{stratum}}}\text{area}_{\text{stratum,depth}}$$

Mean weight per length group were calculated based on gillnet catches and pooled for each autumn and spring period for each year for the total Sound area. Furthermore, length–weight relationships were calculated from linear regressions of log transformed length data versus weight estimates. These regressions have been used in the calculation of the herring biomass (Table 1) by inserting the estimated (raised)

number per length group, i.e. the abundance per length group, into these length–weight relationships.

A.3. Procedure for estimating herring abundance per length group and identification of important year classes

Abundance indices of herring length groups were calculated from the combined acoustic integration values according to stock composition from raised catch data from the biological sampling using length-dependant TS values. The mean weight at length has been used to identify important year classes of herring in the Sound from the estimated (raised) length distribution by means of setting these data in relation to mean weight at age from all of ICES Subdivisions 22–24 obtained from the trawl catches in the international acoustic survey in October performed each year in the 1993–1998 period (ICES, 1998).

A.4. Procedure of removal of plankton echoes

Contributions from plankton, air bubbles (from breaking wind waves or wakes from passing vessels) bottom echoes and (other) disturbances were removed, and false bottom detection on dense fish schools/aggregations (typically herring) were compensated for during the judging procedure using the EchoAnn system. Plankton layers were removed by deletion of relevant layers per 1 nautical mile log in the acoustic data or by inserting a filter for small targets during judging. When fish echoes were mixed with plankton echoes the contribution from plankton was estimated by comparing the integration values with values obtained on other close sampling positions with similar isolated plankton recordings not containing fish. In general disturbance from plankton echoes was insignificant.

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Chapter 6

Discussion and conclusions

Usually fish populations are not spatial homogeneous entities, and densities according to size and age are not spatially homogeneous over time as fish may be quite mobile or completely sedentary. Fish distribution will determine the optimal survey design and the type of statistical analysis methods. For example are the assumptions on the underlying distributions in the fisheries research survey data and whether observations are independent or correlated crucial for obtaining precise and unbiased population estimates. In the present thesis, the precision and bias in survey estimates of fish density patterns and migration are described and discussed in relation to the survey design, the survey stratification, and the different survey data analysis methods and data distributions.

Effects of different factors influencing survey parameters needs to be thoroughly identified, categorized and accounted for when estimating fish density and distribution to reduce variance and avoid bias. Alternatively, it is necessary to standardize the surveys and assume that those effects are constant over time or area to minimize the effects of variability in those factors. This means standardization of survey design, survey equipment, survey procedures, and sampling procedures to homogenize survey detection and catch efficiency. It needs to be considered whether those assumptions on constancy in relation to those parameters are reasonable. Otherwise, the survey estimates of relative abundance and density will be subject to unknown noise (unprecise) and bias, and the estimates will be less robust to be used according to their purposes presented in Chapter 1 which require quantitative reliable estimates. Survey bias is the difference between the expected estimated mean and the true mean (i.e. the actual population abundance or relative density). The bias is seldom known but when it is constant, the variance of the estimates is the sampling variance. This is one reason why survey estimates are usually used as relative indices, i.e. if the bias is constant then the relative indices will capture the tendencies of the dynamics of the true mean over time.

In practice, the within survey variability is often used as a measure of the accuracy of the indices (e.g. Godø 1994; Daug et al. 2002; Beare et al. 2003; Kimura and Somerton 2006). If changes in factors affecting accuracy occur fairly randomly, then the survey indices will be more variable, but they will still track the actual trends. If there are persistent influencing factors they will cause the survey indices to be biased proportional to the part of the stock not caught because of this factor (e.g. Pennington and Strømme 1998). If the bias is constant over time, then the surveys will still follow the actual stock trends, but maybe with a biased absolute stock level. A better understanding and categorization of the above will improve the basis for use of research survey information.

Identification of important knowledge on methods for stratifying and analysing survey information is necessary to structure and categorize the general basis for evaluation of survey fishing power and acoustic detection efficiency, as well as to capture the survey variability. Thus, a main question becomes whether the survey measurements (being a trawl haul, gill net set, or an acoustic recording) will give representative data and useful estimates of e.g. the local abundance, density, and distribution of fish, and which intrinsic and external factors may lead to biased or uncertain estimates of CPUE or hydroacoustic abundance. Also, how to sample the population in a representative manner becomes a main question. This involves full consideration of biological traits information, e.g. migration habits and fish behaviour, and external conditions affecting occurrence of fish such as hydrographical conditions and time of day, which all will affect the survey efficiency. To increase the reliability and usefulness of research surveys it is necessary to determine what causes the factors of availability, catch efficiency and selectivity to change, in order to compensate for and optimize in relation to this (e.g. Godø and Wespestad 1993; Godø 1994).

6.1 Analysis of survey data and underlying survey data distributions

Efforts to improve precision of abundance estimates from trawl surveys have been concentrated on two main approaches covering 1) modifications of the estimators, and 2) modification of the survey design (e.g. Smith and Gavaris 1993). Modifications of the estimators involve typically assumptions on the statistical analysis model (model-based-theory) and the underlying data distribution and data transformation to meet the specifications of the statistical model to describe the variability in the survey data in the best possible way. The appropriate survey analysis models depend on the type and design of the survey (design-based-theory) (Kimura and Somerton 2006). These aspects are carefully considered in each of the thesis Chapters 2-5. Some statistical terms used and relevant in the present context are described and defined in **Appendix A**, which the below descriptions refer to.

In relation to estimating uncertainties for groundfish trawl survey estimates of mean abundance ICES suggests to calculate confidence limits of survey CPUE data based on *resampling procedures* such as the *bootstrap method* (Smith 1997; ICES 2007; DATRAS www.ices.dk) where *asymmetric distributions* do not cause problems, covariance between ages is a part of the output, and there are no *assumptions of spatial distributions* or random (or stratified random) sampling. In Chapter 4, such bootstrap analyses are used to estimate observation variability (CV) in Norway pout IBTS CPUE data including measurement errors in the Norway pout indices as calculated and available from the ICES DATRAS. Basically, in the bootstrap method the true sampling cumulative distribution function is replaced with the empirical cumulative distribution function and then it proceeds as if the empirical is the true one (Kimura and Somerton 2006). This is done by resampling the finite population with sample size n, where the n samples are replaced with e.g. 1000 resamplings from the n samples. Such a resampling is equivalent to sampling from the empirical cumulative distribution function. On this basis the mean and standard deviation can be estimated as well as variance and confidence intervals. When sampling is viewed as occurring from an infinite population the bootstrap seems most straightforward to use, however, there is a risk that applying the bootstrap to finite populations will overestimate the variance (Kimura and Somerton 2006). The method is relatively easy to use, and it does not require selection of a probability sampling model except that all observations are equally likely. The bootstrap method can be used both for stratified random and systematic and adaptive stratified survey designs.

Assuming normal distribution and independence between survey observations

Often survey analyses use pre- or post-stratified design where the survey area is sub-divided into strata under the assumption of homogeneous fish abundance and density patterns within the strata, and then mean abundance is calculated for each stratum (and fish age or length group). This is usually the arithmetic mean (e.g. ICES 2007; 2012,a,b). When observations are from highly contagious fish distributions, the usual arithmetic mean is not an efficient estimate of the true population mean (Kimura and Somerton 2006). When calculating simple population means according to a strata or the full population area the simple means are heavily dependent on the underlying data distribution of survey observations and type of sampling design.

Smith (1990) showed how the application of statistical models and their specific estimates to survey data can result in biased estimates of the population means and variances using traditonal sample survey theory (Smith and Gavaris 1993). When analysing survey data with models assuming *normal distribution* of the survey observations it is often also assumed that the observations are *independent.* The fish distribution pattern affects survey accuracy because the spatial distribution of

fish is almost everywhere patchy (Simmonds et al. 1991; Pitcher 1993; Pennington and Strømme 1998; Simmonds and MacLennan 2005). Survey data often violate the normality assumption in three generally recognized ways: abundance of zero values, positive skewness, and occasional extremely large outliers, and it is not easy to find methods of analysis that address these issues and yet allow an analysis that accomplishes the survey goals (Kimura and Somerton 2006). The Probability Density Function (PDF) of the fish density is often found to be positively skewed, which means that a large proportion of the observations yield small values. This type of PDF is very different from the symmetrical *normal* or *Gaussian* PDF on which much sampling theory is based. Furthermore, because of often relatively few survey samples the distribution around the mean may be far from normal. For any stationary PDF, the estimates of arithmetic average and sample variance are unbiased estimates of the true mean and variance. But when the PDF is not *normal* or *Gaussian* these estimators although unbiased are not the most precise. Assumptions of *normal distribution* may result in confidence limits that are narrower than in reality (underestimating actual variation). (Cochran 1977; Simmonds et al. 1991; Smith and Gavaris 1993; Pennington 1996; Sokal and Rohlf 1997; Kappenman 1999; Pennington and Strømme 1998). Other distributions may describe survey data better, and enabling a more precise estimation of the mean.

Survey data distribution and transforms methods (as addressed in Chapters 2, 4 and 5)

When modelling survey data more efficient estimators can be derived if the PDF is explicitly known or can be transformed to a known distribution such as the Gaussian PDF. It is important to determine the appropriate transformation, and the transform theory assumes that samples are drawn from a stationary PDF, that the PDF is unimodal, that the PDF is known or correctly estimated. Also, zeros should be real zeros due to an absence of fish. The transform method is (in most cases) not suitable for contagious distributions unless they conform to the assumptions of Aitchesons method (Aitcheson 1955) which treats the zero values and non-zero values as samples from different PDFs, and the estimators are modified to take account of the proportion of zeros in the data.

Continuous distributions (as applied in Chapter 5 and Chapter 4):
Myers and Pepin (1990) investigated the robustness of log-normal-based estimators of abundance (*logarithmic transformation*) under the assumption that the individual survey observations are independent, irrespective of trawl position, and they belong to a *continuous distribution*. Such transformations and assumptions were made in the GLM multi-variate analysis of variance applied on herring survey density data in Chapter 5. Logarithmic transformation was applied in GLM analyses of Norway pout mean weight and mean length at age survey data in Chapter 4 (Lambert et al. 2009 from which the results are used in Nielsen et al. 2012) with *gamma distribution* (see below). Also, the GLM analyses of logit transformed maturity data (to obtain proportions mature between 0 and 1) in Chapter 4 follows a continuous distribution. The variation in magnitude of observations (e.g. large catches) caused by fish aggregations, i.e. exess of zero catches and/or a few very large catches, can dominate the total survey estimate, skew the distribution to the right, and cause great heteroscedasticity (Kimura and Somerton 2006). In such cases, usual normal theory tools are not applicable, and the *log transformation* can tame effects of large catches, skewness and heteroscedasticity making it efficient in survey data analysis (Kimura and Somerton 2006). Log transformation generally stabilizes the variance but often the resulting distribution is far from normal and the true confidence limits may be larger than those based on normal theory. (Pennington and Grosslein 1978; Pennington 1983). A few very small catches can make the lognormal distribution based mean estimate a very poor one (Kappenman 1999). Estimating the mean abundance on the original scale requires attention because the simple anti-log of the mean on the logarithmic scale is often a biased

estimate of the mean on the original scale (Kimura and Somerton 2006). Since the distribution on the original scale is typically skewed to the right, the median might be the preferred measure of the central tendency (Kimura and Somerton 2006). Estimation on normal scale requires that data follow a multivariate normal *continuous* distribution, and this assumption is often not fulfilled in survey data because of a discontinuity with zero catches. In general, continuous distributions have problems with inclusion of 0-observations, i.e. zero catches. (Lewy and Kristensen, 2009). The logtransformation (catch+constant) has been applied to avoid this problem, however, this procedure is also problematic because the results of the parameter estimations are very much influenced by the choice of the constant (Lewy and Kristensen 2009). The density data analysed in Chapter 5 did not contain zero-observations or few very small density observations, and it did follow a continuous distribution given the acoustic transects. Concerning, independence between the density observations in Chapter 5, i.e. uncorrelated acoustic backscatter between transects by stratum, there is referred to the survey stratification discussion in Section 6.3.

A slightly more refined alternative is the use of *delta distributions* (Pennington 1983), i.e. extensions of the log-normal distribution (Stefánsson 1996), where zero values are modelled separately and the positive values are assumed to be *log-normal (or gamma) distributed* (Pennington 1983; 1986; Pennington and Strømme 1998). Application of the *delta-log-normal distribution* to highly contagious distributions appears an attractive alternative to simple arithmetic mean which is not a efficient estimate of the true population mean because of the skewness, large outliers, and large number of zero value problems (Kimura and Somerton 2006). The assumption of the *delta-lognormal distribution* is that there is a positive but unknown probability that the observation is zero, and given that the observation is positive, it is drawn from an unknown lognormal distribution (Kimura and Somerton 2006). Aitchison and Brown (1957) provide estimators of the mean and variance of the delta-lognormal distribution. The *delta distribution* is not so sensitive to an occasional large catch/sample sizes leading to more narrow confidence limits, and the mean in the delta-distribution is a more efficient estimator when the non-zero values are well approximated by a *lognormal distribution* (Pennington 1983; Smith 1988; Caveriviére 1993; Pennington 1996; Pennington and Strømme 1998; Daug et al. 2002). Pennington and Strømme (1998), which follow up on the methodology presented in Pennington (1985) and Pennington and Godø (1995), estimates CPUE indices with a simple time series technique where the whole survey time series is used to describe a point of the population p (CPUE) by the autoregressive integrated moving average (ARIMA) process as originally described in Box and Jenkins (1976), and where the *delta-log-normal distribution* is used to estimate the mean. Here the correlation between observations of the population over time (but not in space) is partly integrated. The method may not be fully efficient for small sample sizes. (Smith 1988; 1990; Myers and Pepin 1990; Pennington and Strømme 1998; Syrjala 2000). Whenever the mean on the logarithmic scale is back-transformed to the original scale, the potential for severe bias exist (Kimura and Somerton 2006). More recently the Tweedie distribution (Tweedie 1984) has been suggested as an alternative to the the delta distributions to be used in e.g. generalized linear models analyses (Candy 2004; Shono 2008; Berg et al. 2014).

Stefansson (1996) combined the *delta-gamma distribution* with GLM modelling of groundfish survey data where the model simultaneously analyse zero and non-zero haul data. Here presence / absence (0/1) data is modelled as binomial, and the nonzero data as gamma. The model estimates the probability that an observation (station) is greater than zero, and the gamma parameters for the mean can be linear models of position, depth, etc. The gamma parameters are estimated using maximum likelihood. (Stefansson 1996; Kimura and Somerton 2006). The *gamma distribution* is a two-parameter family of continuous probability distributions based on positive observations.

Discrete distributions (as applied in Chapter 2):
Discrete valued distributions such as Poisson distribution of observed catch in numbers (e.g. Taylor 1953), the negative binomial distribution (e.g. O'Neill and Faddy 2003; Lewy et al. 2004; Kristensen et al. 2006; Cadigan 2011; Chapter 2, Nielsen et al. 2013) and the Log-Gaussian Cox Process (LGCP) (e.g. Kristensen 2009; Lewy and Kristensen 2009; Chapter 2, Nielsen et al. 2013, Nielsen et al. 2014) have recently been developed further and been used in the statistical analysis of survey data (Chapter 2).

In Chapter 2 (Nielsen et al. 2013) a size-based generalised linear model (GLM) analysis has been applied assuming negative binomial distributions and overdispersion. Here a *negative binomial distribution* and log (the canonical link function) of the CPUE as a linear function of the parameters has been tested, i.e., assuming that the logarithm of the mean is linear. This allows for inclusion of 0-observations as all discrete valued distributions (CPUE rounded up to the nearest integer), i.e., zero catches of fish by length. If the assumption of negative binomially distributed data hold, an over-dispersion parameter (compared to the Poisson distribution) is estimated. When fish aggregations cause excess of zero observations and/or a few very large catches the data can be assumed to come from a negative binomial distribution (Kimura and Somerton 2006). On the small scale, observations from a random non-aggregated process are usually thought of as being distributed as Poisson, where the mean and variance are equal (Kimura and Somerton 2006). Consequently, density in one full survey area is assumed to be Poisson, but if there are spatiel density gradients the survey area can be considered as subareas. The distribution of density within each of the sub-areas is assumed Poisson while the between area density is gamma distributed. The combined model Poisson and gamma is the negative binomial distribution where the variance is larger than the mean. Aggregated distributions in surveys can often be approximated by the *negative binomial distribution* where the mean and variance are related by $var = mean + mean^2/k$ and where the parameter k describes the degree of spatial density variability in different sub-areas (of the overall survey area) in the negative binomial distribution. Small values of k imply extreme aggregation with large variance, while the Poission variance is the limit as k goes towards infinite. Taylor (1953) found for non-aggregated populations that are distributed as Poisson the size of sampling unit should be statistically irrelevant, and that for negative binomial distributed populations then the shorter the tow, the more efficient the sampling design. In Chapter 2, the CPUE data were not standardized to 1-hour hauls because the negative binomial distribution is not well suited to handle such standardisation. Bisell (1972) extended the negative binomial model to allow for varying element size which is useful when analyzing trawl data with different tow duration (Kimura and Somerton 2006). Short tows have e.g. been used in Chapter 2 where the negative binomial distribution was also applied to inter-calibrate survey trawls (see below).

Some models directly use the information in the dependence and *correlation between observations* and use *discrete distributions* in survey data to describe fish distribution and density as used in Chapter 2. The Log-Gaussian Cox Process (LGCP) model provides densities with high resolution in time and space for survey data (Kristensen et al. 2013; Chapter 2). It is a flexible counting model describing the *discrete catch in number* of observations which account for the spatial and other correlation and dependence between catches and observations (Diggle and Tawn 1998; Møller et al. 1998; Diggle and Ribeiro 2007; Kristensen 2009; Lewy and Kristensen 2009). The model uses the *multivariate Poisson-lognormal distribution* (Aitchison and Ho 1989) where catches are *Poisson-distributed survey observations* with the *mean densities following a multi-variate lognormal distribution* (Kristensen et al. 2013). The Poisson process can be regarded as the sampling process generated by the fishing or detection process, e.g. the observed numbers caught in a haul, given the

density is assumed to follow a *Poisson distribution*. The mean densities in the sea are assumed to follow a *multivariate lognormal distribution* in which the spatial correlation between densities is included by assuming that correlation in densities is a decreasing function with distance between them. That is, the model utilizes that the correlation between numbers caught increases when the distance in space and time between them decreases, and that the correlation between size groups in a haul increases when the difference in size decreases. The model can handle zero observations because of the *discreteness* of the LGCP. Over-dispersion compared to the Poisson distribution can be handled by the model as well. The method does not need stratification of data, but is to some extent sensitive to survey stratification targeting certain densities of species or size groups.

It should be noted that age-disaggregated survey indices of abundance (as used by e.g. ICES) are typically not discrete valued. It is common to use either lognormal errors or a *multinominal distribution* when investigating numbers that by nature are counts, but this does usually not take into account over-dispersion (e.g. long right tail distribution) because fish show aggregating behaviour, i.e. individuals do not behave as independent individuals (Hrafnkelsson and Stefansson 2004). Also, there is often correlation between counts in e.g. length groups. Often models which do not include over-dispersion will not adequately describe observations such as the Poisson model for random encounters (Kristensen et al. 2006). Hrafnkelson and Stefansson (2004) propose a hierarchical model based on an extension of the *multinominal distribution* where a logistically transformed multivariate Gaussian distribution of *counts in discrete scale* cm-groups is used to account for overdispersion and for different correlation structure in data from surveys of heterogeneous populations. This model is called the *Gaussian-multinomial model* which capture complex covariance structures of categorized length data.

Other studies have investigated fish distribution patterns and their variability by using a single point, the centre of gravity, as an overall measure to describe changes in spatial distribution (Rindorf and Lewy 2006). However, if the spatial distribution of stock abundance in an entire area has to be studied then other methods are required.

Integrating larger scale correlation between survey observations (as applied in Chapters 2 and 5)

On the larger scale, fish aggregations can be thought of as densities varying in two-dimensional space, and one can expect that observations will be spatially correlated dependent on the distance between observations, i.e. a statistically stationary process where the spatial correlation increases the closer the observations are to each other (Kimura and Somerton 2006; Chapter 2, Nielsen et al. 2014). If data are sampled at a scale that is greater than that which spatial correlation occurs, then the usual univariate statistics with independent observations should be applied. Spatial correlation depends very much on the species and size groups, and the scale of the survey. (Kimura and Somerton 2006; Chapter 2).

In order to avoid assumptions of independent observations *geostatistical methods and the kriging methods* have been used where the kriging accounts for larger scale spatial correlations in trawl and acoustic survey data (e.g. Cressie 1989; Cressie 1993; Pelletier and Parma 1994; Diggle and Tawn 1998; Rivoirard et al. 2000; Petitgas 2001; Wieland and Rivoirard 2001; Stelzenmüller et al. 2005; Diggle and Ribeiro 2007; Chapter 5). Classical statistics are suitable for stochastic processes but often ignore the larger scale spatial structure which can bias the results. This can be overcome by calculating mean and variance with adjustment for autocorrelation in the data or use of cluster analysis. Here spatial characteristics of the distribution are attempted eliminated. In contrast,

geostatistics are designed to take advantage of the larger scale spatial autocorrelation by calculating the mean and spatial variance of the data from a variogram which is a plot of the variance (e.g. Simmonds et al. 1991; Rivoirard et al. 2000; Diggle and Ribeiro 2007).

Kriging is a geostatistical method of interpolation used to estimate survey density on a uniform grid where data are collected from a more arbitrary spatial sampling (Kimura and Somerton 2006). Geostatistics requires assumption of stationarity of the distribution. The mean and variance is *independent* in a given point, and sampling variance in each point is the small scale "Nugget" effect (e.g. within haul or station variability). Different types of interpolation are used in geostatistics such as point or block kriging, involving interpolation according to surrounding point observations (of given number) or interpolation of the observations within a block. Geostatistics can be applied both to systematic sampling or stratified random sampling (e.g. Simmonds et al. 1991; Petitgas 2001; Diggle and Ribeiro 2007), and the intention of geostatistics is to obtain estimates from data having *nonuniform* sampling. Hydroacoustic surveys often sample along transects and the sampling will most often be quite nonuniform relative to two-dimensional space (Kimura and Somerton 2006). Kriging has been applied to hydroacoustic survey data (e.g. Petitgas 2001; Chapter 5) in order to improve estimates from *nonuniform continuous sampling*. In Chapter 5, point kriging was used to produce contour plots of herring density obtained from combined acoustic and gillnet surveys based on a systematic survey design in acoustic transects. The surveys were conducted on general dense and high abundance herring occurrences in a rather narrow survey area indicating that the assumption of stationarity is valid. Often it is assumed that the mean is the true mean so that all structure can be modelled as spatial stochasticity. In geostatistics, the semivariogram is typically estimated empirically, followed by smoothing after a choice of a parametric covariance function (Kimura and Somerton 2006), and the exponential and spherical functions appear to be more robust than the Gaussion (Cressie 1993). Ordinary kriging is characterized by the more realistic assumption that the mean is an unknown constant, and the goal is to provide a linear unbiased estimate of the mean (e.g. Wieland and Rivoirard 2001; Kimura and Somerton 2006). The unknown mean value considered would be the arithmetic mean (or alternatively the weighted mean) of values at every location within the domain. Kriging is essentially the linear predictor of the data values on a surface conditioned on observing other values. The usage of geostatistics is accordingly more narrowly applicable to surface estimation. (Kimura and Somerton 2006). A problem here is that the kriging methods for parameter estimation requires that data follow a multivariate normal *continuous* distribution, and this assumption is often not fulfilled (Lewy and Kristensen, 2009). Lai and Kimura (2002) comparee classic randomized complete block design (RCBD) and random field linear models (RFLM) in survey data analysis associated to discrete survey sampling and under assumption that observations near to each other are positively correlated and under assumption of normality. RFLM is essentially the usual fixed effects normal linear model but with the covariance matrix parameterized to allow for spatial correlation (Kimura and Somerton 2006).

The LGCP model (Kristensen et al. 2013; Kristensen 2009; Lewy and Kristensen 2009; Chapter 2) estimate relative abundance in any geographical point (independent of survey stratification), and take account of both large scale and small scale spatial correlation in survey observations, based on spatial correlations between *discrete observations* from surveys. In Chapter 2 (Nielsen et al. 2013), an extension of the LGCP model is applied to the BITS data, but with a further extension in the form of following individual cohorts using correlation in their distribution over time to describe the distribution and density patterns of settled 0- and 1-group Baltic cod. Furthermore, in Chapter 2 (Nielsen et al. 2014) the model is extended in two other ways. Instead of assuming a original (natural) scale size correlation, the model is improved to allow for a transformed length scale. Further,

the spatial and size dependent correlation *between species* is now included, i.e. multi-species interactions. Accordingly, it include correlation in time, space, size and species. The model does not assume that observations are independent, but accounts for correlations, and provide unbiased estimation of densities which depend on the distribution in the entire area. It enables modeling of separate small- and large scale variations in distribution. That is, it estimates the large scale variance due to spatial variability and the small scale variance due to e.g. local fish movements. Given the correlation between observations it is in analogy to the kriging method possible to predict and interpolate unobserved densities at any location in the area. Here the best unbiased prediction of any function of the unobserved density is the conditional mean given the observations and maximum likelihood optimization and estimation of the parameters. (Kristensen and Lewy 2009).

The size correlation in The LGCP model (Kristensen et al. 2013; Chapter 2, Nielsen et al. 2014) is estimated according similarity in distribution between fish of different size. An underlying structured function is fitted to the fish size scale (length axis) to allow the length scale to be transformed. The distribution of fish may be correlated to each other according to distance in size on a linear (natural) length scale, but the correlation may be better explained by looking at correlation between fish in relation to distance on a non-linear transformed length scale (length axis). That can be where size correlation between distribution of fish of different length is better described when the distance in length is on a logarithmic length scale (e.g. that 1 and 5 cm fish are less correlated than 50 and 55 cm fish as 1/5 > 50/55, i.e. the less proportion between lengths the more similar distribution). Given the distribution patterns of the fish, a logistic transformation of length may be better, e.g. where distribution of the small fish are similar and distribution of the large fish are similar, but distribution in the in between length groups are more dissimilar because of fish size specific migration patterns (Chapter 2). Any size correlation can be included in the model for example also covering a free structure according to size with a mean value per size group.

The large scale variance describes the variance around the observed means of survey estimated fish densities according to factors investigated (time, space, etc.), which are assumed to be the true means of fish in the sea given maximum likelihood estimation. Maximum likelihood optimization is used for parameter estimation in the model which allows for estimation of abundance in certain areas and it allows prediction and interpolation of unobserved densities at any point in space as well as goodness-of-fit tests. The principle is that a co-variance function is fitted according to an overall mean of the densities and includes the covariance in observations according to space, time, size etc. In areas, periods, or parts of the population (e.g. certain size groups) not well covered by the observations, i.e. where there are few or no observations, (or between observations in space, time, size) the fitted statistical co-variance-function and density curve can predict the density. The uncertainty estimate on the small scale parameter, i.e. the Nuggett effect, is the interval within which a new observation would be if the trial / sampling / observation was repeated at the same station or locality (i.e. another haul). That is the small scale variation in fish density due to local fish movement and fish behavior and varies from observation to observation, e.g. the haul-to-haul-variation. This movement is dependent on time and space and describes the small scale local movements of the fish and small scale behavior of fish. As explained in Chapter 2, the $\mu(s_i)$ model parameter includes the combined effect of large scale size distributions in the sea and the selection in the catch process (including gear selection, duration of haul and other global effects of the catch process). Thus, the model allows for estimation of selectivity according to the gear and the catch process by following size groups over time in a certain population area. The $\mu(s_i)$ is constant and independent

of time and space. In Nielsen et al. (2013, Chapter 2) the model follows cohorts of a species, while in Nielsen et al. (2014, Chapter 2) it follows length groups of different species.

If the fish behavior in the catch process is different from haul to haul, i.e. fish reacts differently, then the small scale parameter will include a part of the survey catch or detection efficiency according to behavior caused by the catch process and the detection equipment. However, if the fish behavior is constant for all survey observations, then this will not be included in the small scale parameter. By using a model with *discrete observations* and estimation of correlation between discrete observations and with parameters estimating the small scale, large scale, and selection effects the survey catch or detection efficiency has been disentangled according to those specific processes. If at the same time using standardized survey design and sampling procedures eliminating several intrinsic and extrinsic parameters affecting the survey detection and catch efficiency, as well as robust inter-calibration between survey time series and observations, an extensive part of the survey catch or detection efficiency has been included and taken into account, but not all. The variance in the catch efficiency due to the small scale effect and parameter, can be explored further to describe its distribution better and potentially minimize this effect (see also suggestions for future studies in Chapter 2).

Modeling relative abundance using covariates (as applied in Chapters 2, 4 and 5)

Observations and catch rates from surveys can be influenced by several external factors (e.g. environmental factors, fish behaviour, etc.) and detection process factors (e.g. gear specific parameters) as described in Chapter 1. When external factors apart from changes in abundance affect the catch rate, these need to be corrected for in order to obtain an unbiased survey estimate (Berg et al. 2014). The goal is to identify factors influencing the survey detection or catch rates (and efficiency), i.e. covariates which can be related to the rates, and estimate relative abundance indices that have been adjusted for these factors (Kimura and Somerton 2006). Here, more advanced methods such as generalized linear models (GLMs), generalized linear mixed models (GLMMs), and generalized additive models (GAMs) have been applied to correct for effects such as spatial position, depth, and time of day (e.g. Stefansson 1996; Petrakis et al. 2001; Piet 2002; Adlerstein and Ehrich 2003; Maunder and Punt 2004; Venables and Dichmont 2004; Beare et al. 2005; Berg et al. 2014). The GLM and GAM types can have a variety of possible sampling distributions, but the advantage of GAM is that it can fit covariates as smoothed functions whose forms may not be specified (Kimura and Somerton 2006; Woods 2006).

The GLM approach described by McCullagh and Nelder (1989) and Chambers and Hastie (1992) is a flexible way of analyzing survey data with covariates. The method allows the response variable to have a variety of possible distributions such as Poisson, binomial, gamma, negative binomial, etc. This is done by providing an appropriate link function and variance function according to a matrix of covariates and regression coefficients, and parameters are estimated (calculated) using maximum likelihood estimation (Kimura and Somerton 2006). Stefansson (1996) used the delta-gamma distribution and a GLM link to make maximum likelihood estimates of parameters, and a similar approach was used in Chapter 2 (Nielsen et al. 2013) with generalized linear models having negative binomial distribution, overdispersion and log as link function to analyse variance with respect to co-variates. In Chapter 5, GLM was used to analyse mean herring density in geographical strata with respect to spatial, temporal, and environmental covariates. Here logtransformation was applied to change a multiplicative GLM model to a *linear additive model* where density follow a *continuous distribution.* This model can handle unbalanced data where the number of observations

vary by cell. As there were no 0-observations log-transformation was, used and the model residuals were tested for normal distribution. In Chapter 4 (Lambert et al. 2009; Nielsen et al. 2012) GLMs were used to analyse growth and maturity dynamics of Norway pout. Here maturity ratios by age, sex, quarter and area was studied with a GLM using a logit transform, i.e. logit as the link function, and enabling estimation of over-dispersion (dispersion parameter > 1), i.e. binomial distribution. In Chapter 4, also mean length and mean weight at age was analysed with a GLM with respect to a number of explanatory variables where the *gamma distribution* was applied. Finally, the relationship between the maturity ratio and the mean length at age was evaluated statistically using a *binomial model* where logistic maturity ogives were fitted to the percentage maturity data by length class or age group to provide L50 or A50 (length or age at which 50% are mature). Density dependent growth and maturity of Norway pout was furthermore studied by use of GLM in those studies.

The GAM approach is a sort of regression of a variable on the smoothed residual responses on explanatory variables (Kimura and Somerton 2006). In Berg et al. (2014) a GAM-fit was made to the distribution of the geographical strata means estimated from survey catch rate data covering the full population area. The stratification of data and strata size can be chosen freely according to number of observations in each geographical strata (or by stratification by fish size groups instead). Some strata and parts of the population will have many survey observations to calculate means over and for other strata there will only be very few or no observations. The main principle in the GAM method is that the distributions and the curve for the mean values per strata are fitted to a function instead of just using the estimated averages per stratum given the number of observations (and very few observations in certain strata). This function then also gives a (good) description of the mean in strata where there are only few or no observations. GAMS permit non-linear smooth relations between the response and explanatory variables, so spatial stratification can conveniently be replaced by smooth functions of geographical coordinates (splines) (Berg et al. 2014). There is a trade-off between loss of spatial resolution due to the assumption of homogeneity within strata and problems with few or missing values if too fine grained spatial resolution is used. In GAMs this trade-off problem is replaced by an easier problem of smoothness selection for the splines (Berg et al. 2014). Chapter 2 and 5, Pecuchet et al (*In press*) uses GAMS on North Sea and Baltic Sea fish stock-recruitment residuals to investigate trends between stocks. GAMs can succesfully handle non-linear relationships that likely occurs for processes between the marine environment and fish recruitment. Dependence on temperature can potentially be described as a parabola with an optimum value (Woods 2006). GAMs usually perform better than parametric approaches for recruitment and physical environment relationships (Megrey *et al.*, 2005). In Chapter 3 and 5 (Pecuchet et al. (*In press*)), a backward selection is used to retain the best model according to the General Cross Validation (GCV) score which can be used to give higher weight to the number of degrees of freedom (DF) in order to avoid a too large number of explanatory variables and overfitting (Kim and Gu, 2004; Woods, 2006).

6.2 Inter-calibration of trawl surveys and standardization of survey data time series

Sometimes it is necessary to introduce new survey vessels or survey equipment, or calibrate vessels or gears within an international research survey for various reasons (e.g. new survey vessels or new equipment or because manufacturers simply do not manufacture the trawls anymore). To assure standardization and comparability of survey time series it is necessary to compare the catch efficiency (fishing power) and the selectivity of the old and new vessels or gears because their operation highly influence survey detection and catch efficiency (Chapter 2). Typically, this is done by esti-

mating conversion factors that allow historical catches to be expressed in units compatible with the new standard in order to use the full survey data time series (e.g. Robson 1966; Doubleday and Rivard 1981; Ehrich 1991; Warren 1997; Pelletier 1998; Munro 1998; Wildebauer et al. 1998; Lewy et al. 2004; Kingsley et al. 2008; Cadigan and Bataineh 2012). Catch efficiency is size (and species) dependent, so inter-calibration and conversion factors correcting for fishing power differences need to be estimated and calculated on species and size specific basis. A method for inter-calibration of trawl survey CPUE data has been developed in Chapter 2 where the concept of disturbance by one trawl haul in relation to the next was developed and quantified when calibrating new and old survey gears. Here fishery is at the same location to avoid assumptions on a homogeneous population at different (close) locations.

Inter-Calibration of trawl survey data time series (as addressed in Chapter 2)

In a review, Pelletier (1998) classifies calibration of trawl survey gear as either (i) paired haul methods where stations close in time and space are selected on the tacit assumption that fish density is the same (e.g. Sissenwine and Bowman 1978; Wilderbauer et al. 1998; Tyson et al. 2006; Cadigan and Bataineh 2012) or (ii) area based methods where independent hauls are selected within particular geographical strata, where the fish density and size structure are assumed to be homogeneous (e.g. Byrne and Fogarty 1985; Ehrich 1991; Ehrich et al. 1994; Wantiez 1996; Fox and Starr 1996; Huse et al. 2000; Cotter 2001; West 2002). In Chapter 2, the first method is applied. For example, comparative analyses of differences in survey vessel fishing power under the ICES IBTS survey have been conducted on area basis (e.g. ICES 1992). Also, Cotter (2001) applied a statistical model calculating conversion factors between survey vessels and seasons by analysing and fitting log-transformed IBTS indices covering the full survey area taking year class distributions and total mortality for the different fish species into account. Pelletier (1998) found that paired hauls better control the heterogeneity in fish abundance over space and time. The efficiency of randomized complete block designs will generally be preferred by statisticians for the analysis of paired hauls where e.g. two or more vessels fish side by side because the catch ratios then can be compared directly as simple means or totals (Kimura and Somerton 2006). The statistical methods used for estimation of conversion factors should allow for skewed catch distribution and also consider the existence of zero catches by length group. Two estimation methods can be used, either (i) parametric or semi-parametric with assumptions on underlying data distributions or (ii) non-parametric with methods and sampling theory which require no assumptions about data distribution (Cochran 1977; Ehrich 1991; Pelletier 1998; Salthaug 2002). The latter produces simple estimators for the conversion factor, but information on potential influencing factors (e.g. spatial effects, or sequence effects) cannot be estimated with statistical certainty. This results in increased sampling variability, because every tow within a sampling area is assumed to be drawn from the same probability distribution (Pelletier 1998).

Despite the difference in survey design, the estimation of conversion factors and estimation of relative fishing power between vessels have in several cases been based on classical statistical methods, i.e., lognormally distributed catch rates combined with linear models (e.g. regression analysis) accounting for gear and location and haul effects (e.g. Robson 1966, Sissenwine and Bowman 1978; Byrne and Fogarty 1985; Wilderbauer et al. 1998; Chapter 2). Robson (1966) used factoral analysis of variance and least squares regression to estimate fishing power and standard error (based on tests of normal distribution of errors with a mean of 0 and constant variance). Other estimates are based on the relationship between CPUE of two gears (Kappenman 1992; Warren 1997; Wilderbauer et al. 1998). Kappenman (1992) developed an estimator based on the assumption

that the shapes of the distribution functions of the CPUEs of the paired gears are identical except for a scale parameter proportional to the estimated relative fishing power, and Wildebauer et al. (1998) also applied this estimator among 4 different methods (estimators) tested. Kappenman (1992) used a modifycation of the arithmetic average CPUE as estimator where 0-values have been removed and extreme high and low values were downweighted. Stømme and Iilende (2001) used simple proportional indices calculated directly from the paired haul CPUEs. Warren (1997) applied a log-linear model based on the logarithm of the CPUE ratio between the paired hauls, and excluded hauls with 0-catches for all fish length classes. However, to deal with 0-catch in (only) some length groups, Warren (1997) used a mixed delta-Poisson distribution in the modelling. For a paired trawl design where two vessels are trawling at the same time with a distance ranging from 0.25 to 1 nautical mile, Pelletier (1998) applied a quasi-likelihood method for estimating relative fishing power between the vessels assuming that the mean values of the abundance associated with the paired hauls are identical. This method allows for inclusion of 0-catches for one of the vessels in the comparison, but not for the other. Here the relative fishing power estimate is obtained by dividing the total catch by vessel summed over all paired hauls with each other, and Pelletier (1998) suggests bootstrapping of this statistic (with reference to Smith 1997). Overall, this bootstrapping method seems superior to the classical block analysis of variance since the parametric normal distribution assumption and log-transformation is not required here (Kimura and Somerton 2006). Also, Warren (1997) used bootstrap distributions for estimating the precision of the conversions. Wilderbauer et al. (1998) analysed survey data covering a wide depth range and found for that case that fishing power was more precisely estimated by the methods that explicitly used the paired hauls. However, a number of papers have demonstrated considerable spatial variability in catch rates between nearby stations (e.g. Ehrich 1991; Kvist et al. 2001; Chapter 2), implying that nearby hauls can not be assumed to cover exactly the same population, which means that the benefits of paired nearby stations vanish, since the performance of the traditional paired hauls method heavily depends on this assumption (i.e. that densities are stationary and drawn from the same statisitical distribution) . Further, in practice selection of stations is difficult, because information on the small scale spatial distribution of the resource populations is rarely available in advance (Chapter 2).

Chapter 2 considers a special case of the paired haul design where the successive hauls are taken in the same track line within a short time range where it is acknowledged that the first haul affects the fish density available to the second haul. This design has previously been used for trawl gear comparison (Wildebauer et al. 1998; ICES 2002) and for comparing different coastal gears (Methven and Schneider 1998). However, fishing in immediate succession in the same track (Chapter 2) creates a new problem, as the first haul may affect the fish density available for the second haul by removing fish or inducing changes in behaviour that alters the distribution and density. This effect, which is termed the disturbance effect, therefore needs to be estimated and accounted for. The disturbance effect caused by the first haul is assumed to be dependent on the gear actually used but being independent of fish density and habitat. This disturbance effect, therefore needs to be estimated and accounted for. The net effect of removing the fish caught and changing the fish behaviour includes both attraction of fish to and repulsion of fish from the track line, so the disturbance effect can be both positive and negative (Chapter 2). Sensitivity to the finer scale spatial distribution of the fish is also reduced since it can be assumed that relative density and size structures are retained at the station site within the short duration between successive tows.

The method (Chapter 2) uses a generalized linear model and standard statistical techniques that allow i) maximum likelihood estimation of the conversion factor and gear specific disturbance effects for new and old gear, ii) calculation of confidence limits for the estimates, and iii) testing of

hypotheses whether the conversion factor and the disturbance effects differ across (5 cm) length classes and whether they differ from zero or not. The method assumes that the individual CPUEs are independent *Poisson distributed* variables and the derived *conditional distributions are binomial distributed* for each station, length group, and type (sequence of gear), where the *conditional distributions are the distributions of the sum of the CPUEs from the paired hauls*, i.e. where the CPUE from one haul is dependent and conditional on the sum of the CPUEs from both hauls. The linear equation of ln(conversion factor) + ln(disturbance effect1) + ln(disturbance effect2) with *logit as the canonical link function* is used to analyse the paired CPUE data and an *over-dispersion* parameter is estimated if the assumption of *binomial distributed variables* does not hold. Fish density is treated as a nuisance parameter. For the traditional paired hauls comparisons, it is not possible to assess bias and uncertainty of the conversion factors because they depend on the fine scale spatial distribution of the fish sampled upon. Because of the independence of the spatial fish distribution, the new method is preferable to the traditional paired hauls designs (e.g. Pelletier 1998) for which it is generally not possible to obtain the statistical properties of the estimated conversion factors. Wilderbauer et al. (1998) ignored the disturbance factors but attempted to balance out the sequence of haul effect by splitting their survey effort equally between type 2 and type 3 experiments (Chapter 2). However, by ignoring the disturbance effects, the conversion factor would be overestimated by 64% (see Chapter 2).

The estimated disturbance parameters are related to the size of the catch as reflected by the catchabilities and by the size of the fish (here cod and flounder (*Platichthys flesus*)), and it is assumed that they (and the conversion factors) do not depend on any station or habitat characteristics, i.e. the type or number of stations covered (Chapter 2). However, it cannot be precluded that catchability and disturbance differ systematically across habitats, and if the differences are identified as important, the experimental design and the model should be changed accordingly. Kingsley et al. (2008) applied a similar type of intercalibration experiments and statistical model with use of consequtive hauls of two different survey trawls for shrimps (*Pandalus borealis*). These analyses indicated density dependence in the estimated disturbance effects, i.e. that catch in the second haul relative to that in the first haul depends not only on the gear used, but also on the fish density, where the second haul catches being a smaller proportion of the first catches when densities were high, and often larger than the first catches when densities were low. This can, however, also be a habitat difference in catchability and disturbance rather than density dependence.

Cadigan and Bataineh (2012) found a negative binomial model appropriate for analysis of paired count data from comparative fishing studies (two vessels or gears) where the variance is a quadratic function of the mean. They compare the results of an ordinary unconditional negative binomial model and a conditional negative binomial model. They found that estimation with an unconditional (ordinary) negative binomial model can result in biased estimates of the over-dispersion in presence of many nuisance parameters. Accordingly, they propose 3 ways to deal with nuisance parameters in the conditional negative binomial model. The method in Chapter 2 was applied to implement the new BITS survey design using a carefully designed sequence of tracks (Nielsen et al. 2001b; ICES 2002). In Chapter 2, an overdispersion parameter is estimated which is significantly higher than 1. No 0-catches were observed in those trials, however, a few hauls in which the total number of fish caught was less than 20 individual were excluded. The conversion factors (inter-calibration parameters) obtained have been implemented in the Eastern and Western Baltic cod stock assessments (e.g. ICES 2002; 2012b) and in scientific investigations of Baltic cod stock distribution and density patterns (e.g. Chapter 2, Nielsen et al. 2013). In general, Munro (1998) argues for use of a decision rule on whether to apply relative fishing power corrections (or not) based on the mean

square error on the conversion factor. He argues that if the estimate of the correction factor has a lot of uncertainty then the error on the estimate of mean CPUE could actually become worse by correcting data, even for a statistically significant fishing power difference.

6.3 Survey design, stratification and standardisation of survey effort allocation

In general, fish tend to aggregate forming contagious and patchy distributions (Simmonds et al. 1991; Pitcher 1993; Pennington and Strømme 1998; Simmonds and MacLennan 2005; He 2010). The degree of contagion varies according to species, stock, size and life stage, time of year/day, distribution of food organisms and predators, and environmental conditions. The distribution patterns of the target species and sizes need to be considered and understood when designing a survey. For a fixed sample size, the precision of an abundance estimate depends on the spatial distribution of the stock, resulting in less precision the higher variability in the spatial distribution. Survey precision will increase if the survey region can be divided into strata in which the densities of fish are more homogeneous, however, usually, little is gained by having too many strata.

Standardization of survey stratification and sampling design (as addressed in Chapters 2, 4 & 5)

All results in Chapters 2-5 are dependent on and discussed in context of the survey and experimental design from which the analysed data are obtained, and the investigations in Chapters 2 and 5 have directly involved development of new research survey design to improve the precision of the research survey estimates according to the aims of the studies.

For all trawl and acoustic surveys, including those used in Chapters 2-5, the precision, accuracy, and bias of survey estimates of abundance and density is highly dependent on the survey design and effort stratification scheme with respect to the target species distribution. The survey detection and catch efficiency is dependent on the survey coverage and design, as well as on the standarddization of the design and sampling procedures. Furthermore, the design is necessarily linked to the analysis of data collected. An optimal design will generate data and estimates which have 1) the desirable statistical properties such as consistency, lack of bias and minimum variance, 2) allow objective evaluation of the precision of the sample results, and 3) allow comparison of the precision between different designs and modified designs. The precision of any survey will depend on 1) dynamics and variability of the fish population under study and factors affecting it, 2) the number of sample units, and 3) the survey design and the method of data analysis. (e.g. Cochran 1977; Pennington and Grosslein 1978; Johannesson and Mitson 1983; Shotton and Bazigos 1984; Fogarty 1985; Simmonds et al. 1991; Sokal and Rohlf 1997; Beare et al. 2003). Methods of increasing the precision of a survey estimator always involves the sampling plan (Smith 1990). Rotherham et al. (2007) addressed the latter point 3 by developing a strategy for sampling based on a) identifying suitable sampling gears for target species, b) testing different configurations of equipment and sampling practices to ensure that samples are optimal, representative and cost efficient, c) understanding scales of spatial and temporal variability, and d) cost-benefit analyses to optimize replication.

To obtain an unbiased estimate of the population it is important to select a survey design covering the full population and the targeted species and size groups (Walters 2003). Partial coverage of the fish distribution area requires strong assumptions on the abundance in the areas not covered and may lead to a severe bias in the abundance indeces (Walters 2003). The assumption of similar abundance trends by species and size/age as in the covered areas may have severe consequences,

and it should be taken into consideration that commercial fishery can deplete some areas before moving their effort to other areas (Walters 2003). This may affect survey catch rates by area if not taken into consideration in the survey coverage and design. This means that it is best to design the survey to cover the population in a window or snapshot in time and space with relative stability in population distribution where the full population is available (Simmonds et al. 1991; Simmonds and MacLennan 2005), and that both commercially fished and non-fished areas are covered. Migration periods and migration route areas are inappropriate for a survey snapshot because of risk of covering some fish several times or totally miss some fish because of movements. To have coverage in only commercial fished areas may over-estimate the stock if the commercial fishery only allocate effort in high density areas, or under-estimate the stock if the commercial fishery deplete the stock in certain areas. The geographical limits of the survey area must be defined. The survey area and geographical coverage is usually selected according to 1) national boundaries, 2) physical boundaries (coastlines, lakeshores, etc.), 3) suspected distribution and range of target species and sizes, 4) oceanographic conditions (sea ice, ocean currents, hydrographical stratification, etc), and 5) available resources and sea days which limits coverage to only certain areas. Limitations in the area coverage results in 3 choices according to abundance index estimation and data analysis which is either 1) refuse to construct an overall stock trend index but restrict analyses to the covered areas, or 2) assume that mean estimates for the covered areas are representative as well for the non-covered areas and fill in means from the covered strata into the non-covered strata, or 3) fill empty cells (strata) with best estimates of what would have been seen in those cells, which for example can be done by using several sources of information such as indices from other surveys in other seasons, fishery information, or other information filling in a time-space table of abundance indices to indicate the best choice (Walters 2003). Bad assumptions in relation to the two latter possibilities will severely bias abundance indices (Walters 2003).

Scientific surveys are usually based on standard effort allocation design, sampling design and standard sampling equipment including associated procedures according to a robust statistical analysis method and design (e.g. Fogarty 1985; Simmonds et al. 1991; Godø 1994; Nielsen et al. 2001b; Beare et al. 2003; Simmonds and MacLennan 2005; Kimura and Somerton 2006; ICES 2002; 2011; 2012a,b; 2013a,b,c). Survey *standardisation* aims to keep as high precision – and as low potential bias - of survey estimates as possible between and within surveys. That is to keep the effort stratification, equipment/gear, vessel, operation procedures, processing protocols, and sampling design as constant as possible from survey to survey to minimize sampling variability and increase accuracy. On this basis, observed changes in biological parameters, size and age structures, and densities / abundances are assumed to reflect actual changes in the living populations with reduced bias or with known constant bias. For stock assessment and forecast it is essential that survey year class indices are comparable between surveys and years (e.g. Berg et al. 2014).

Stratification is the process whereby a survey area is divided into subareas or strata. Higher precision in survey indices can be obtained by increasing the number of observations. Another way of reducing the variance and increase precision is to apply (standardized) stratified sampling. If the total area is divided into several strata and the strata are chosen properly, populations within strata will be more homogeneous than in the total survey area. Using a randomized design within each stratum, the sampling stations or transects will be more evenly distributed. It is not necessary that the strata represent perfectly homogeneous or uniform areas of fish abundance, but the strata should be chosen so they are at least more homogeneous than the overall survey area. (Cochran 1977; Shotton and Bazigos 1984; Sparre et al. 1989; Fogarty 1985; Simmonds et al. 1991; Hilborn and Walters 1992; Kimura and Somerton 2006).

Trawl survey stratification and design and standardization with respect to allocation of stations (as used in Chapters 2, 4 and 5)

The estimation of total biomass from trawl survey CPUE involves several crucial assumptions and considerations among other in relation to survey design. Early reviews of theory are given in Alverson (1971), Mackett (1973), FAO/UNDP (1975), Gulland (1975), Saville (1977), Flowers (1978), Doubleday (1981), Grosslein and Laurec (1982), Sissenwine et al. (1983), Fogarty (1985), Gulland (1988), Sparre et al. (1989), FAO (1992), Hilborn and Walters (1992), and Beare et al. (2003). Katsenevakis et al. (2012) give an overview of sampling and survey methods dealing with imperfect detectability and variable detectability in surveys. The basic assumption for using trawl surveys in fisheries advice is that the abundance of fish is related to the catch of the trawl given a certain survey effort and catch efficiency (catchability) and a given population the survey equipment meets, i.e. the absolute abundance. As the full catch in a standard survey haul is known the average catch per tow (per unit of effort) may be related to fish density, and the survey catchability relationship can consequently be defined as the relationship between the catch per unit of effort (CPUE) and the true density (D). The survey catchability can be categorized according to the availability of fish to the survey which is the average proportion of the population within reach of the survey, and the detection efficiency, i.e. the average proportion of the available fish which is retained or detected. By *standardized surveying* the detection efficiency is assumed constant. (Modified from Godø 1994; Godø and Wespestad 1993; Godø et al. 1999). The efficiency of a survey generally refers to the variance of the estimated indices of abundance (Kimura and Somerton 2006).

Random versus systematic and adaptive sampling design and stratification within strata:
It is not possible to guarantee unbiased estimates of the mean abundance within any stratum except by choosing sampling sites completely at random where each site has equal probability of being sampled. If samples are taken along transects, e.g. parallel to (rather than across) some biological gradient, within the stratum there is a risk of getting observations, which will only be representative for a part of the gradient and thus misleading. (Cochran 1977; Gulland 1988; Krebs 1989; Hilborn and Walters 1992; Sokal and Rohlf 1997). Cochran (1977) discusses 3 designs of allocation of samples, i.e. the i) *total random design*, ii) the random design with strata (*stratified random design*), and iii) *systematic design* throughout the areas. Here sampling is either conducted systematically, e.g. in transects or over a grid, or locations are randomly selected. *Totally random sampling* in the full survey area is a poor way to sample aggregated populations because samples themselves may be aggregated and the population aggregations over-or-under estimated (Kimura and Somerton 2006). Populations are typically distributed in different habitat areas, and it is desirable that the different types of areas are sampled to some extent. Stratified sampling is best when we know in detail how abundance and variance vary among strata, however, this varies from species to species. When several species are targeted systematic design may sometimes be more appropriate when variability occur at the scale of the survey (Kimura and Somerton 2006). In relation to the precision of *systematic versus random sampling* then the estimate of the mean from a *systematic sample* is more precise than the estimate from a *random sample* if and only if the variance among observations within the *systematic sample* is less than the variance among observations from a *random sample*. Consequently, the *systematic sample* mean density will be more precise (though the estimate may be biased) if the systematic transect or station grid is oriented so as it take into account spatial or temporal gradients so that its observations are less variable than would be obtained by randomly chosing sampling points while ignoring the gradients. On the other hand, if the systematic sample density observations are more variable than would be obtained by random

sampling then it will be less precise than the random sample, and probably also be biased. (Cochran 1977; Gulland 1988; Hilborn and Walters 1992; Sokal and Rohlf 1997).

Many surveys target several species (multi-species surveys) and several life stages (size groups) of fish, and a survey design being optimal for one species/group may be sub-optimal or inefficient for another given different gradients as explained above. Both a *stratified random* and *systematic survey design* provides uniform coverage of many species in a survey region, even if the spatial fish distribution varies from year to year (e.g. Godø 1994). In a *stratified* survey area, if the amount of sampling within a given stratum is dictated by the size of the stratum, this is called *proportional effort allocation*. Area proportional distribution of the effort assures that the entire survey region is covered fairly uniformly with no targeting of specific species and size groups. (e.g. Chapter 5; Gunderson 1993; Godø and Wespestad 1993; Godø 1994; Godø et al. 1999; Nielsen et al. 2001a; Daug et al. 2002; Beare et al. 2003; ICES 2013a,b).

It is well known that the precision of an abundance estimator will depend on the degree of sampling coverage and the homogeneity of the fish distribution. Therefore, if a priori information about the variability within the strata is available, it may be more appropriate to assign more sampling to those subareas of higher variability in an attempt to increase overall precision. As variability often changes over time such a priori information often needs to be real time information and within the same survey. This is called optimal allocation or an *adaptive survey design*. In practice, when stratum variances are unknown, an assumption is made that stratum variance is proportional to the stratum density. In effect, areas of higher density are allocated more sampling.

Systematic survey design:
A *systematic survey design* usually cover the survey area uniformly either by transects or through even sampling in strata, but where fishing stations are not selected at random, i.e. it will usually distribute the effort evenly throughout the survey area (Cochran 1977; Simmonds et al. 1991; Godø 1994). There are usally gradients in fish densities, and a systematic design may more easily determine those, however, all gradients need to be known to reduce the risk of orientation along an unknown gradient. Fish abundance is likely to vary on several scales in space and time (e.g. shoaling or schooling fish), and it is generally impossible to cover all scales adequately witin a single survey (Hilborn and Walters 1992). A systematic design will 1) be more cost efficient in terms of ship time and sample point location, 2) permit precise mapping of spatial patterns of density and boundaries of distribution, 3) minimize the risk of missing density concentations, and 4) facilitate comparisons of distribution and density patterns over time. If the grid points are too far there is a risk of missing density concentrations (e.g. a school) or another biological gradient or a risk of influence by periodic density variation between grid points, but this risk is also there for a random sample of the same size. (Cochran 1977; Krebs 1989; Simmonds et al. 1991; Hilborn and Walters 1992; Godø 1994; Sokal and Rohlf 1997). An disadvantage of systematic sampling is that the variance (precision) of the sample mean cannot be assessed from data on variation among observations within the sample. It is usual to apply simple random sampling formulas to the observations (Kimura and Somerton 2006). The only safe way to determine the precision of the mean of a systematic sample is to gather repeated samples at randomly chosen transect or grid station starting points, and then look directly at the variation among the means of these samples. (Cochran 1977; Hilborn and Walters 1992). If more than one systematic sampling design occur in a broader sampling design then the systematic samples (i.e. clusters) can be thought of as chosen at random and the variance between their means used to estimate a sampling variance (Thompson 2002; Kimura and Somerton 2006).

Cochran (1977) warned against having too many strata in a systematic design. When optimizing an Atlantic cod survey using average abundances measured from previous surveys Smith and Gavaris (1993) noted that survey precision could better be enhanced by allocation of tows to strata rather than through improved strata definitions. In Chapter 5 a systematic design is used targeting all size groups of one species (herring) in a combined acoustic and gillnet fishery survey stratification. Here sampling of acoustic data associated with multi-mesh-size gillnet fishery sampling were done in a rather narrow survey area (the Sound) sub-divided into 13 smaller strata for which mean herring densities were calculated by stratum. The acoustic transects covered the full survey area and all sub-area-strata in an approximated proportional effort allocation design, and both high and low herring density localities were covered by the transects. The continous acoustic sampling along fixed closely placed transects was conducted on monthly repeated basis during 27 surveys spanning over a 6 year period. The starting point in the acoustic transects was chosen at random for each survey (however depending on wind and current conditions). It was assumed that sampling was from a finite population. Associated fishery (gillnet) stations (Chapter 5) were covering each stratum at each or every second survey according to this systematic stratified sampling design. The gillnet catch rates from the systematic design were not used to calculate total abundance and density indices, but only to obtain representative species and size distributions to be applied to the acoustic data. The gillnet selectivity by length group was estimated (Chapter 5, Poulsen et al. 2000) to obtain true size distribution of herring. Total abundance by length group was calculated based the acoustic estimates where the species and length distributions from the fishery was applied to acoustic target strengths (TS) and the mean area back scattering strengths (Sa), and hereafter herring length-weight functions were calculated and applied to obtain density in weight per area unit (Chapter 5). Finally by multiplying the known area for each stratum with the respective mean densities, which were then summed, the total biomassfor the full survey area was obtained for each survey (Chapter 5).

Stratified random survey design:
Many trawl surveys in e.g. the North Atlantic uses a *stratified random design* and survey standardization according to this (e.g. Godø 1994; Beare et al. 2003; ICES 2012a,b; 2013a,b). Also this has been used in South-East Asian trawl research surveys (e.g. Daug et al. 2002). The allocation of strata considers several factors and biological gradients such as i) fish abundance and density, ii) homogeneous fish distribution and population composition within a stratum, and iii) adequate coverage of the full survey and fish distribution area and all depth strata. The survey effort allocation (e.g. hauls and detection stations) within each stratum are chosen randomly, and the number of survey observations (survey stations) and the sample size within a stratum is for example adapted to the variability in abundance, density and population composition. The characteristics judged to be best for the construction of strata is the frequency distribution of the variable of interest, e.g. survey CPUE (Cochran 1977).

Some surveys keep a *stratified random sample design* with allocation of a fixed number of hauls within a predefined and/or similar size geographical strata such as the ICES IBTS survey (Chapter 4; www.ices.dk; Beare et al. 2003; ICES 2011; 2012a; 2013a). Here the stratification is based on a grid of ICES statistical rectangles (administratively and multi-species defined blocks of one degree longitude x 0.5 degree latitude ~ 30x30 nautical miles ~ 56x56 km). Each rectangle is usually fished by the ships of two different countries so that at least two hauls are made per rectangle. The positions of the 2 hauls within each rectangle are fixed from survey to survey. The fishing positions should, in theory, be chosen at random. In practice, however, many vessels fish at more or less at fixed positions to minimize damage to the trawl. The fixed positions were initially random selected through a stratified random design. In the early 1970s, IBTS haul duration was standardized to 30

minutes, and the design is also standardized according to day-night sampling with exclusive day sampling. Since a major goal of surveys is to provide interannual trends in abundance it can be argued that those trends is best estimated if the same stations are chosen every year (Kimura and Somerton 2006). However, Warren (1994) argues that an exclusive fixed station design can lead to biased estimates of both annual abundance and interannual trends, and suggests that at least some stations are chosen by random. The results of the analyses of the Norway pout population dynamics (Chapter 4) is dependent on the ICES IBTS survey stratification covers the full Norway pout stock distribution area representatively, and that filling in empty cells for the IBTS survey based age-length keys for Norway pout is correct when using the best available survey information from surrounding areas. The coverage of areas influence the efficiency of a survey design, and therefore stations are often allocated in proportion to the area of a stratum and then selected individually by random within this stratum. Such a stratified random survey design with a *proportional effort allocation* according to the area of depth strata within larger geographical areas is used in the ICES BITS survey (Chapter 2). In the new ICES BITS survey design, the major part of the hauls (60% of the total number of hauls across nations in a quarterly survey) are stratified according to the areas of certain depth strata within larger geographical units covering the Baltic Proper, and the hauls are randomly pre-selected within those strata from a tow library before each and every survey (Chapter 2). Furthermore, as the spatial distribution of the different targeted groups typically changes over time as for example in cod (ICES 2002; 2012b; 2013b), then additional allocation of the remaining hauls (40%) are stratified according to high abundance and density areas of cod estimated from recent years (e.g. 5 years) (Chapter 2). This is done to increase the coverage of areas with higher variability, and also those additional hauls are selected at random for each survey from a tow library. According to the BITS survey manual, stations with no or low oxygen concentrations (< 2 mg O_2 / ml) do not need to be trawled and sampled given the assumption of no demersal fish occur at such localities (ICES 2012b; 2013b). Such an assumption may bias the catch efficiency estimates as it has been shown that among other juvenile cod occur at such locations in the Baltic Sea covered by the BITS survey, and this survey is very much targeting juvenile cod (Chapter 2).

When using recent years running means of the density distributions of the targeted species as a part basis for effort allocation it introduces the capacity of adjusting the allocation scheme on a continuous basis to be best adapted to the medium term variability and changes in distribution patterns over time (Smith and Gavaris 1993). This is also often a function of having fewer strata and, therefore, more sets available for each stratum to optimize allocation according to density patterns. Furthermore, when using several recent years running mean densities it downscale the year-to-year variability as well as take into consideration more long and medium term regime shifts in general distribution, e.g. long periodical trends in changes in distribution according to e.g. hydrographical patterns or general abundance/density dependent distribution patterns (e.g. Smith and Gavaris 1993; Chapter 2). However, it is important that all areas are still covered even if there are empty samples, so "black wholes" of knowledge do not occur as fish are very mobile (and fishermen may argue that the fish are there in fisheries management context) (Hilborn and Walters 1992; Walters 2003). Gavaris and Smith (1987) and Smith and Gavaris (1993) introduced a stratified random survey design in the eastern Scotian Shelf demersal trawl surveys based on historical spatial distribution of cod to improve precision of the survey abundance estimates compared to previous simple depth based random sampling. The haul allocation scheme was based on historical averages for several earlier survey years of spatial distribution of abundance, which was more robust and gave higher precision than only use of data from the most recent year. This was done to optimize the allocation of the available number of trawl sets and to obtain better coverage of the target species and size/age groups. Optimum allocation of sets to strata is to allocate the sets in proportion to the survey

estimate variability within the strata. Smith and Gavaris (1993) also used *post-stratification* of historical surveys and estimated the variability with definition of new strata boundaries which were more closely related to the spatial distribution of targeted species and sizes in previous years. Furthermore, survey re-stratification according to variance and precision was compared for different seasonal coverage in the survey (summer, spring) according to uniform and non-uniform distribution differences of cod between seasons. Dressel and Norcross (2005) used post-stratification of trawl survey data according to habitat types which gave more precise and less design-based abundance estimates compared to an unstratified estimator. Jardim and Ribeiro (2008) used geostatistics to test two sampling designs of hybrid-random-systematic and systematic design for hake (*Merluccius merluccius*) where they overlayed the random stratified survey samples with a regular grid to create the hybrid, and where the systematic survey had 4 strata. In this comparison they found a lower CV for the hybrid, and that this design overall performed better. Chen (2004) coupled systematic grid based survey designs to a model assisted empirical likelihood analysis method using loglinear regression and non-parametric smoothing to reduce standard error of survey abundance estimates.

Adaptive survey design:
Kimura and Somerton (2006) define *adaptive sampling designs* as those allowing the design to change according to what is found as the sampling progresses. There are several types of adaptive survey designs, and when animals are rare and clustered in their distribution the adaptive design seems attractive (Kimura and Somerton 2006). Adaptive cluster design is typical when stations are initially placed randomly, and those stations that find targets of interest with abundance over a certain fixed level become center points of additional search stations and so forth until the sampling algorithm is exhausted (Kimura and Somerton 2006). Francis (1984) proposed a two stage sampling design using an adaptive approach with an initial sample of trawl sets in ongoing surveys to estimate the variability in abundance, and accordingly optimize the stratification of the rest of the hauls in the same survey according to this variability. This assumes that all main densities are covered in the initial part of the survey which may be difficult not having enough hauls available for doing this in the adaptive design. Also, it is necessary to analyse the survey data real time to estimate the initial variability. Besides, those problems pointed out by Francis (1984) there are other drawbacks of the adaptive survey design when making total biomass estimates such as 1) vessel movement is extremely time consuming and costly as the vessel must go back to sample the adaptive sampling stations, 2) the adaptive sampling scheme must proceed to stations around the "edge" of concentrations, 3) needs real time decision on whether an occasional high catch rate is an outlier or not (i.e. can the spatial correlation be detected over the high variability that exists in fishing observations and how informative is a sample about the catch rate in neighboring sampling stations?), and 4) on what basis is the criterion value (threshold) chosen for additional adaptive samples (Kimura and Somerton 2006). When adding stations to those that can be considered a random sample the simple mean of all observed (including adaptive) samplings is not an appropriate estimator of the population mean, and in this situation different estimation methods have been proposed (Kimura and Somerton 2006). Hanselman et al. (2003) evaluated that adaptive cluster design was an advantage when surveying Pacific ocean hake (*Merluccius productus*). In a simulation study of survey design for yellow perch (*Perca flavescens*), Lake Erie, USA, Yu et al. (2012) compared the simple random, the random stratified and the adaptive-two-phase sampling designs. When comparing the bias, variance of the mean, and the mean squared error (MSE) the adaptive design performed best, and among different types of adaptive designs tested (adaptive two-phase sampling, adaptive cluster sampling, and adaptive two-stage-sequential sampling) the first type performed best (Yu et al. 2012). In a combined acoustic-trawl presence/absence survey design the acoustic transect sampling can be used to provide information on the abundance of the patches,

and trawl stations can estimate background density outside patch areas (trawl stations in patches are excluded), which can be a time-efficient survey method (Everton et al. 1996; Kimura and Somerton 2006). However, a problem here is to distinguish when surveying (trawl/acoustic) in a patch or not.

Standardization of (combined) acoustic and fishery survey design and stratification of effort (as applied in Chapters 2 and 5)

Acoustic surveys are widely used for estimating indices of pelagic fish stocks as well as for squid and krill (nekton and plankton) (e.g. Simmonds and MacLennan 2005). Survey design and analysis in the field of fisheries acoustics has been reviewed by Johannesson and Mitson (1983), Shotton and Bazigos (1984), Simmonds et al. (1991), and technical and methodological aspects of fishery acoustics and acoustic research surveys are reviewed and summarized by Simmonds and MacLennan (2005). While fisheries surveys provide point estimates with direct sampling of fish with a certain fishing gear operated in a certain period at a station, then acoustic sampling is conducted on continuous basis over transects with integration of reflected acoustic energy and single target reflection to either count or estimate aggregate biomass from a known volume of water. Both types of survey produce geo-referenced estimates of density and abundance (Kimura and Somerton 2006). The stratification of the acoustic surveys and the extension of coverage is central in order to cover the full target population and sizes, i.e. its full distribution area in a certain time window. This is key in obtaining a survey estimate of mean density and abundance corresponding to the true mean in the population, and as such also central for the survey detection efficiency and bias herein. First of all acoustic surveys require 1) well calibrated survey equipment, 2) knowledge of the scattering properties of the targets which give the echoes, and 3) an understanding of how the acoustic samples relate to the whole stock distribution patterns and evaluation of variability. Given this, the basic assumption is that the abundance of fish is related to the acoustic backscatterring energy detected for a certain area. When insonifying the water column with acoustic energy at a certain frequency from a moving vessel then the timing and the strength of return echoes from the insonificaiton is dependent on species, size, position, depth, and orientation of the target, as well as hydrographical factors (Chapter 3), in the water column. The species and size compositions of the targets are typically obtained from associated fishing gear sampling in the acoustic scattering layers, e.g. by trawls, gillnets, or longlines (e.g. Simmonds et al. 1991; Simmonds and MacLennan 2005; Kimura and Somerton 2006; Chapter 5; Chapter 2; Chapter 3). In acoustic surveys, the samples are integrals over depth of echo-intensity (backscattered acoustic reflection energy) averaged over many transmissions. The general principle is that the echo integration system provides output in form of acoustic backscatterring volume values, S_V, over a certain water volume and/or the acoustic backscattering area values, S_A , over a certain area which can be e.g. a square nautical mile (nmi^2) or a larger geographical stratum. The strength of the echo of an individual fish is the target strength (TS). The mean TS by geographical area unit (e.g. by nmi^2 or by larger geographical stratum) is estimated according to species and size distribution in weighted proportions of occurrence of species and length groups in the raised catch by stratum from the associated fishery sampling. When dividing the mean S_A with the mean TS according to species and size distribution the abundance in total number of targets (fish, N) by species and size group and area is obtained (see Chapter 5, Nielsen et al. 2001a Appendix A; Simmonds and MacLennan 2005).

Typically, the acoustic surveys are conducted as *acoustic transects* covering the survey area for target species and associated with representative fishing gear sampling of fish species and size compositions of the vertical acoustic scattering layers (e.g. Simmonds et al. 1991; Simmonds and MacLennan 2005; Chapter 5; Chapter 2). A full transect can be a sample, or an area unit can be a

sample, e.g. echo integration over e.g. 1 or 5 nm (= 1 log) according to a certain stratification of the survey area and the transects. Many authors have addressed the questions of where to place transects and the best *acoustic track design* with respect to optimal form and direction according to fish distribution and movement to obtain the most efficient estimates of average biomass or abundance (Simmonds et al. 1991; Simmonds and MacLennan 2005; Kimura and Somerton 2006). This includes evaluation of whether predetermined systematic parallel track or zigzag track design is better compared to random parallel sampling (Simmonds et al. 1991; Simmonds and MacLennan 2005). It is obvious that the track design is statistically coupled with the method of data analysis. Simmonds et al. (1991) conclude that in an open sea or wide shelf survey area systematic parallel tracks are preferable with high transect density (transect density = numbers of crossings of the same sampling area). Parallel tracks can be utilized to eliminate the component variance from only one direction, and they provide maximum separation and least correlation between transects (Francis 1984; Simmonds et al. 1991). In line with Kimura and Lemberg (1981), they also conclude that the systemic zig-zag design is preferably when transect density is low, i.e. a small number of transects in a narrow survey area, as for example used in the narrow Sound area (Chapter 5). However, the zigzag design has the disadvantage of increased and, thus, uneven oversampling in the vertices (or turnarounds) of the zig-zag-transect. A fully random sampling scheme and track stratification is not recommended, although providing valid confidence intervals, because it can possibly leave large portions of the survey area un-monitored, and possibly also can allocate tracks so close that some fish are monitored twice under the same survey. Random design should only be used in a 2-stage approach where the area of interest is pilot surveyed widely spaced to detect regions of high density. However, the adaptive design where the track design is adapted during the survey, i.e. a not pre-planned survey design, is not recommended unless it is done in a 2-stage approach. As all fish stocks show evidence of temporal change, and in a 2 stage approach both the pilot survey and the adaptive (or the above random) transect may miss some parts of the stock, the estimates will be biased. The adaptive approach may, however, be a possibility in case of very high contagion. (Simmonds et al. 1991; Simmonds and MacLennan 2005). Jolly and Hampton (1990) proposed using quasi-random transects, and Simmonds and Fryer (1996) concluded that a systematic design with kriging provided the most precise survey estimate, but a stratified random survey with at least two transects per strata is necessary to obtain reliable variance estimates (Kimura and Somerton 2006) as done in Chapter 5. Simmonds et al. (1991) set up a table with the following recommendations according to pre-planned track design in relation to the type of survey area, stock distribution pattern, and whether sampling from the same statistical distributions:

Narrow Shelf/Fjord:	Low / High contagion	Systematic zigzag
	Non-stationary	Systematic zigzag w. stratification
	Very high contagion	Outline followed by systematic zigzag
Wide Shelf/Open Sea	Low / High contagion	Systematic parallel
	High contagion	2-stage random parallel
	Non-stationary	Systematic parallel w. stratification
	Very high contagion	Outline followed by systematic parallel
		Adaptive design.

It should be noted that according to Cochran (1977) the systematic sampling requires a random starting point to estimate and unbiased mean and variance, and this is usually not followed in acoustic surveys. However, both in Chapter 5 and Chapter 2 this criterion has been followed. Another issue of systematic sampling is that if the population is not randomly distributed in the survey area, or according to the selected strata, then there is no valid (consistent or unbiased) estimator of variance

in contradiction to surveys which are random stratified. Both for acoustic transects as well as for the sequence of trawl hauls in a trawl survey the direction of surveying according to the direction of fish movement is important and result in a Doppler shift effect and bias of the survey estimates and accordingly affect survey detection efficiency if not taken into account. (Cochran 1977; Simmonds et al. 1991; Sokal and Rohlf 1997; Simmonds and MacLennan 2005). Only if the backscatter between transects is uncorrelated the variance and coefficient of variance of mean abundance can be estimated simply from random sampling formulas where the sampling unit is the individual transect (Kimura and Somerton 2006). Williamson (1982) suggest to use cluster sampling formulas where the individual transects is considered an independent cluster sample. This approach is criticized by Francis (1984) because the spatial process being sampled is not station, however, it should be noted that geostatistic methods also generally assume spatially stationary processes (Kimura and Somerton 2006) when used for analysis of acoustic data such as kriging to estimate spatial explicit densities and abundances as used by e.g. Wilson et al. (2003) and in Chapter 5.

Standardization and stratification of associated fishery sampling to the acoustic survey sampling: The abundance and density estimates from acoustic surveys are directly influenced by the catch composition by species and size class from the associated sampling with fishing gears (e.g. Simmonds et al. 1991; Simmonds and MacLennan 2005; Chapter 3; Chapter 5; Chapter 2). Trawl is by far the most common gear used in relation to species and size class allocation to mixed acoustic recordings. The size and species composition of the catch should be representative of the fish population in the area and in the backscattering layers, and ideally the fishing gear should have the same efficiency in catching the different species and sizes, which is not the case. The relative species and size compostion of the associated fishery are directly influenced by the availability of the target species and sizes to the fishery, the fish behaviour to the catch process, and the selectivity of the gear influencing the survey detection and catch efficiency. The fishery surveys associated to the acoustic surveys give only relative distribution of targets because only a part of the total area recorded by the acoustic equipment is covered by the fishing gear. It is often impossible to obtain as many fishing samples as necessary for a reasonable precise and accurate estimation of the population structure. The acoustic recording is continuous and cover the full water column in transects, i.e. more systematic, while the fishing sample is only point samples at certain selected stations in certain depth layers according to either a certain stratification or according to post-stratification targeting the main acoustic backscattering layers (see Section 6.4). Consequently, the fishing methods may influence precision and introduce some errors and biases in the surveys, i.e. species and size group allocation error, which are much higher than the errors coming from the acoustic data (Simmonds et al. 1991; Simmonds and MacLennan 2005). Therefore, the weighting of biological sampling in relation to the acoustic sampling during an combined acoustic and fishery survey should be based on how variable (mixed) the species and size composition is compared to how variable or evenly the fish densities are distributed and in relation to the fishing method used (Simmonds et al. 1991; Simmonds 2003; Simmonds and MacLennan 2005). Post-stratification can be efficient in multi-species surveys since different post-stratification schemes can be employed for different species provided there is a clear basis for post-stratification, e.g. a systematic survey design or some known factors or gradients the different species distribute according to.

Even though procedures generally are standardized in international acoustic surveys different methods for coverage of the water column of the acoustic transects and the fishery sampling of the vertical acoustic scatter layers exist between countries and time periods within those international surveys (e.g. ICES 2012b; 2013b). For example the new standard and recommendation for the IBAS (International Baltic Acoustic Survey) has since 2012 been that the acoustic S_A-value shall

cover the total water column and the fishery sampling shall cover all vertical acoustic scatter layers. In case of two or more scattering layers are present in one area, it is recommended to sample all layers by the same fishing operation, i.e. to fish in the different layers with the same duration in each layer for each fishing operation (ICES 2012b; 2013b). Previously, there have not been standards for this design of survey coverage introducing variability in acoustic data with respect to the coverage between different vessels participating in the survey and between different survey periods. Another problem is diurnal migrations and differences in distribution, where fish on or very close to the seabed during day will be excluded from the acoustic survey detection (cannot be distinguished from the acoustic backscatter from the seabed), and when being more pelagic distributed and available to the acoustic detection during night then they may have changed (visual determined) trawl selectivity. This problem has been dealth with in Chapter 5 (see below). Ideally, the acoustic and fishery sampling should be fully comparable according to diurnal vertical migrations and take that into account in the stratification, which is not always the case and not allways standardized in the surveys between vessels (e.g. IBAS).
The associated fishery to the acoustic sampling performed for herring in the Sound (Chapter 5) was performed with scientific overview-gillnets specially designed and equipped with panels of several mesh sizes of herring gillnets to cover all size classes of herring and for which herring size selection parameters could be calculated (Chapter 5, Poulsen et al. 2000). This fishery was conducted during night overlapping the acoustic sampling in the different strata and also stratified according to depth. Given coverage of both deep and shallow areas in the narrow Sound area it was not possible to conduct representative trawl sampling. The acoustic-fishery survey design for intensively monitoring herring in the Sound was carefully considering the distribution patterns and behaviour of the herring to obtain representative samples (Chapter 5).

A part of the sampling of juvenile Baltic cod in Chapter 2 was based on continuous acoustic monitoring in acoustic transects stratified to cover a selected part of the Bornholm Basin and associated bank areas. This include selected shallow, medium depth and deep stations (areas) where juvenile cod distributions patterns were investigated. The transects were not used to calculate total abundance in the area, but only to analyse relative density differences of cod by length group. The associated fishery was performed with several types of hauled gears (pelagic and demersal rigged trawls and several types of young fish trawls) which intensively and repeatedly covered many associated fishing stations and several depth layers both during day and night (Chapter 2).

6.4 Standardization of estimation procedures and data processing methods from acoustic survey detection

Judging and partitioning of acoustic survey data (analysis, post-processing and weighting as addressed in Chapters 2, 3 and 5)

The post-processing, often called judging, of acoustic survey data can be divided into two main processes. The first step is to remove non-fish contributions from plankton layers, air bubbles (e.g. from the propeller of the survey ship or other ships), bottom/seabed, and noise from ships/propellers, etc. The second step is to allocate, assign or partition the contributions considered due to fish according to the echogram and/or to the distribution in associated fishery (e.g. trawl) samples. Based on these contributions density and abundance of the various species and size groups can be estimated in the different strata of the survey area.

Judging:
Most often the judging is based on the appearance of the recordings on the echograms, which will determine the proportioning. Single targets, schools and layers of specific strength and frequency dependence can be identified in the data processing, while echoes from plankton and plankton layers needs to be removed. Echoes from dense plankton layers may occasionally totally mask the fish echoes. As plankton usually has lower target strength than fish then adjustment of threshold settings in the acoustic data sampling or in the post-processing of the acoustic data will often be necessary. Bottom echoes for which the strength will depend on seabed hardness needs to be removed as well as air bubles and noise from the ship or propeller. Even though standardized procedures in the international surveys and survey manuals are described to some extent (e.g. ICES 2013a,b), the judging is usually done by individual scientists. This means that judging and data partitioning is a highly subjective process. There will inevitably be inconsistencies between different scientists nationally and internationally that introduces uncertainty and in the worst case bias and introduce inaccuracy in the acoustic survey detection estimates over time. In Chapter 3, Chapter 5, and Chapter 2 the judging of the acoustic data time series was performed by the same scientists to minimize this possible bias and uncertainty.

Assignment and partitioning of the fishery data to the acoustic estimates:
Acoustic surveys very often target several species and size groups which have highly variable acoustic target strength properties (e.g. Simmonds and MacLennan 2005; Chapter 3 and references herein). The echo integrals are partitioned to the species and size classes using the information obtained from the associated fishing operations. In many acoustic surveys, the between haul variations in length composition by species will be small compared to the between species variation, i.e. relatively homogeneous size composition compared to the species composition (Simmonds et al. 1991). Statistical robust models for the assignment and partitioning to the fishery information are not available (Simmonds and MacLennan 2005; ICES 2012b; 2013b), and a main problem here is the interpolation and weighting between the sampling points of fishing stations (Simmonds et al. 1991; Simmonds 2003). Simmonds and MacLennan (2005) proposed three methods for combining the results of fishing stations with different weighting factors in relation to different acoustic survey stratification methods used. The weight given to each sample is dependent on the characteristics of the fish concentration sampled by the fishing gear: a) weight is equal to the proportion in each catch; b) weight is equal to the catch rate in a stratified sub-area; c) echo integrals observed in the vicinity of the trawl stations are used as weight. Overall, they recommend b) as the most generally applicable method. The weighting factors depend on how the fishery catches are considered. If the catch rates in the fishery are assumed to be proportional to abundance then each sample should be weighted according to the catch rate of the species (and size group). If the catch rates are poorly related to abundance, then equal weight to all samples should be given, or weight proportional to neighbouring echo integrator values of the species (and size group). Different methods of assigning acoustic backscattering energy to fish species and size group, i.e. the identification of the echo trace, will give different results and introduce errors and bias in the survey and catch efficiency. In some respects, errors in species allocation are more serious than errors in allocation to size groups in the case where between haul variability of the species compositions is more pronounced than the variability of the length composition. (Simmonds et al. 1991; Simmonds 2003; Simmonds and MacLennan 2005). Consequently, it is important to consider the best method according to the specific survey stratification and design, and it is important to do this in a standardized way between surveys in a data time series. An example of the procedure and principles for estimating fish abundance from combined acoustic and fishery data is described and published in Chapter 5.

Spatial averaging and post-stratification of acoustic data and selection of homogeneous regions:
As described above the aim of geographical stratification in surveys is to achieve a relatively homogenous species and size distribution within the strata so the samples of density values are more homogeneous within a strata compared to the total survey area. The statistical reason for stratifying is to reduce variance and increase precision of the total result. Several spatial post-stratification and averaging methods for acoustic surveys as well as their statistical advantages and disadvantages are described in Simmonds et al (1991) and Simmonds and MacLennnan (2005) as listed below. The elementary distance sampling unit (EDSU) is the length of an acoustic track along which the acoustic measurements are averaged to give one sample. The EDSUs are typically between 1 and 5 nm and the samples are statistical samples which usually are assumed to be internally homogeneous and to display serial (auto-)correlation. The setting of the EDSU should assure minimum serial correlation. The amplitude distribution of density values is usually far from normal. It may be log-normal, and in most cases non-stationary and anisotropic. In acoustics fish density is a stochastic variable with a statistical distribution where the mean is estimated as the average of a large number of observations. The stochastic nature of the density comes from movements of fish and, on a much finer scale, from the intrinsic variability of acoustic propagation of scattering. As such the density is a result of stochastic processes depending on location and time of observation.

Spatial averaging and post-processing methods:
No stratification being the simplest method of calculating abundance or mean density and the confidence intervals based on all EDSUs. The samples (EDSUs or transects) are assumed to be independent estimates in the total area. This will give high variance particularly if the stock is stationary and inhomogeneously distributed. Auto-correlation between EDSUs is not accounted for. It is not applicable on a non-uniform grid, but the grid should be random or systematic parallel.
Complete transect(s) as a single sample where data are one-dimensional and there is low error on each of the transects cumulated data because the transect is exhaustively known. The samples are assumed to be independent within strata. There is no autocorrelation between EDSUs along the transect. Elimination of the along-transect variability results in reduction of sampling variance. It is not applicable on a non-uniform grid, but the grid should be random or systematic parallel.
Stratification in transects where the area represented by one transect is the stratum (EDSU). It is simple to calculate abundance, mean density and confidence intervals. However, variance will be low because of heterogeneous data in each stratum. Auto-correlation between EDSUs (transects) invalidates this method. Non-random positioning of transects will limit the method. It is not applicable on a non-uniform grid, but the grid should be random or systematic parallel.
Stratification in blocks where each block contain several transects or pieces of transects. Strata must be chosen as independent as possible, e.g. based on ecological data. The method tries to take account of autocorrelation between transects, i.e. variance estimation is more reliable when there is autocorrelation between EDSUs. The strata are not constructed from EDSU/transect density values, and the method assumes independence between within strata samples. The distribution of EDSUs as well as the intra-transect variation can be taken into account. Thus, it does not introduce bias into the estimate of precision. It demands more complex statistical methods. It is not applicable on a non-uniform grid, but the grid should be random or systematic parallel. This method has been used in Chapter 5.

Contouring is where the strata boundaries are drawn according to the distribution of one or more parameters which describes the population, e.g. density where the EDSUs are samples of different density levels contoured. It reduces variance due to construction of homogeneous and independent strata (good homogeneity). It partly eliminates autocorrelation problems by partly including auto-

correlation between EDSUs, taking into account the larger spatial structures in the population, and good potential for correlating results with other information (hydrography, fishery, etc.) – as long as this does not introduce dependent and non-homogeneous strata. The method assumes independence between EDSUs within the strata. There are no constraints on the survey design where all types of routes can be used.

Stratification in rectangles where the area of interest is divided into rectangles bounded by lines of latitude and longitude and where the samples in each rectangle are assumed to come from a homogeneous distribution. The rectangles must be large enough to be independent of each other according to anisotropy, and small enough to remain internally homogeneous. Variance will decrease compared to an unstratified method, however, the autocorrelation of EDSUs inside each rectangle is not considered. The EDSUs with each rectangle/strata are assumed to be independent. A way to overcome this limitation is to use large EDSUs. It allows any survey design where all types of routes can be used, as well as combinations of those. Auto-correlation between strata (dependence) shall be minimized.

Geostatistics, e.g. kriging, explicitly includes autocorrelation between EDSUs assuming variance only depends on distance and direction between samples. No requirement for independent samples. It is unaffected of the amplitude distribution (e.g. no requirement for the assumption of normality), but it can be difficult to interpret variograms from highly skewed distributions, and it may be useful to calculate variograms from log-normal transformed data. It is very tolerant to any survey design where all types of routes can be used, as well as combinations of those. Whether the data are stationary or not must be carefully checked because the results will depend on selection of an appropriate geostatistic tool according to this. This method has been used in Chapter 5.

It appears from the above that it is very important to match a particular grid design in survey effort allocation to the specific analysis method. Mismatch between those will severely and directly impact survey detection precision, accuracy, bias and efficiency. Stationarity of the variance and the mean may be coupled (Simmonds et al. 1991; Simmonds and MacLennan 2005) which should be taken into consideration. Often survey data will show dependence between neighbouring samples, which means that the variance estimates tend to be biased. This bias can be reduced by using repeated estimates (e.g. overlapping surveying with two ships in same area), simulated repeated estimates by bootstrapping, or transforming data for more efficient variance estimates, or by directly taking the autocorrelation and dependence into account by geostatistics and cluster analysis methods. The bootstrap method does not take spatial distribution and variability into account.

6.5 Conclusions

The thesis developed and improved methods for the integrated analysis of different types of fishery independent research surveys (trawl surveys, acoustic surveys, hydrographical surveys, and gillnet surveys) to study the distribution, density, abundance, migration and biological population dynamic parameters of marine fish species. The topics in the thesis addressed different combinations of trawl, hydro-acoustic, gillnet, and hydrographical data and application of different survey data analysis methods under consideration of factors influencing the survey catch and detection efficiency. Each topic was investigated in one of more case studies.
One thesis topic has been to provide more precise estimates of fish distribution and density patterns from survey data (Chapter 2). The 1st case study applied advanced statistical methods to Baltic trawl

data and hydro-acoustic survey data in combination with survey sampled hydrographical data to estimate distribution and density patterns of juvenile 0-group Baltic cod. These patterns were largely unknown. In the 2nd case study new methodology was developed for analyzing trawl research survey data for Baltic cod and whiting including the correlation in distribution and density according to space, time, size, and species. The more precise density estimates improve the knowledge of the stock-recruitment relationship of Baltic cod and can improve the Baltic multi-species stock assessment. Furthermore, it will enable more precise marine management and spatial planning involving fish stocks and fisheries in the Baltic Sea. In context of Baltic cod stock assessment, the 3rd case study developed a new method for inter-calibration of trawl survey CPUE data by fish size group exemplified by Baltic cod (and flounder) where the concept of disturbance by one trawl haul in relation to the next have been developed and quantified when calibrating new research survey trawl gears with the former ones. These results have been based on introduction of a new international ICES BITS trawl research survey design.

A second topic was to improve and develop hydroacoustic research survey methods for more precise detection and discrimination of fish species according to fish size and orientation in the water (Chapter 3). Here, the 4th case study focused on more precise acoustic target strength estimation of juvenile cod, while the 5th case study has focused on acoustic discrimination of juvenile gadoid fish in particular juvenile Baltic cod. This enables more efficient research survey estimation of juvenile cod (gadoid) density patterns to be used in stock recruitment estimates and stock assessment.

The third topic was to estimate more precisely fish mortality, maturity, and growth parameters for small forage fish species using research survey information (Chapter 4). Associated to this, the 5th case study analysed these population dynamic parameters using trawl survey data taking into account spatial variation. This study provided more precise estimates and deeper understanding of Norway pout mortality, maturity, and growth dynamics. The more precise population dynamic parameters have been implemented in and improved the North Sea Norway pout stock assessment, management advice, management, and long term management plan evaluations.

The fourth topic was to develop methodology to integrate hydroacoustic, gillnet, and hydrographical research survey data to investigate pelagic fish migration patterns (Chapter 5). The methods were applied in the 6th case study to evaluate Western Baltic herring feeding and spawning migration based on distribution and density estimates in a narrow over-wintering area of the stock. The more precise information on migration patterns gives better possibility for acoustic monitoring of the full stock abundance in different areas and seasons og the year to be used in stock assessment and marine spatial planning. Also, it increases knowledge on biological interactions and mixing with other stocks and species.

In the final synthesis Chapter 6, the thesis reviews relevant analysis methods of research survey data and underlying data distributions, survey design and stratification, trawl survey inter-calibration and standardization, as well as estimation procedures and data processing methods in context of the obtained results and methods developed in the thesis. This is done with focus on survey precision and uncertainty (bias, sources of errors) for trawl and acoustic surveys and factors affecting it.

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Summary

The thesis developed and improved methods for the integrated analysis of different types of fishery independent research surveys (trawl surveys, acoustic surveys, hydrographical surveys, and gillnet surveys) to study the distribution, density, abundance, migration and biological population dynamic parameters of marine fish species. The topics in the thesis addressed different combinations of trawl, hydro-acoustic, gillnet, and hydrographical data and application of different survey data analysis methods under consideration of factors influencing the survey catch and detection efficiency. Each topic was investigated in one of more case studies.

One thesis topic has been to provide more precise estimates of fish distribution and density patterns from survey data (Chapter 2). The 1st case study applied advanced statistical methods to Baltic trawl data and hydro-acoustic survey data in combination with survey sampled hydrographical data to estimate distribution and density patterns of juvenile 0-group Baltic cod. These patterns were largely unknown. In the 2nd case study new methodology was developed for analyzing trawl research survey data for Baltic cod and whiting including the correlation in distribution and density according to space, time, size, and species. The more precise density estimates improve the knowledge of the stock-recruitment relationship of Baltic cod and can improve the Baltic multi-species stock assessment. Furthermore, it will enable more precise marine management and spatial planning involving fish stocks and fisheries in the Baltic Sea. In context of Baltic cod stock assessment, the 3rd case study developed a new method for inter-calibration of trawl survey CPUE data by fish size group exemplified by Baltic cod (and flounder) where the concept of disturbance by one trawl haul in relation to the next have been developed and quantified when calibrating new research survey trawl gears with the former ones. These results have been based on introduction of a new international ICES BITS trawl research survey design.

A second topic was to improve and develop hydroacoustic research survey methods for more precise detection and discrimination of fish species according to fish size and orientation in the water (Chapter 3). Here, the 4th case study focused on more precise acoustic target strength estimation of juvenile cod, while the 5th case study has focused on acoustic discrimination of juvenile gadoid fish in particular juvenile Baltic cod. This enables more efficient research survey estimation of juvenile cod (gadoid) density patterns to be used in stock recruitment estimates and stock assessment.

The third topic was to estimate more precisely fish mortality, maturity, and growth parameters for small forage fish species using research survey information (Chapter 4). Associated to this, the 5th case study analysed these population dynamic parameters using trawl survey data taking into account spatial variation. This study provided more precise estimates and deeper understanding of Norway pout mortality, maturity, and growth dynamics. The more precise population dynamic parameters have been implemented in and improved the North Sea Norway pout stock assessment, management advice, management, and long term management plan evaluations.

The fourth topic was to develop methodology to integrate hydroacoustic, gillnet, and hydrographical research survey data to investigate pelagic fish migration patterns (Chapter 5). The methods were applied in the 6th case study to evaluate Western Baltic herring feeding and spawning migration based on distribution and density estimates in a narrow over-wintering area of the stock. The more precise information on migration patterns gives better possibility for acoustic monitoring of the full stock abundance in different areas and seasons og the year to be used in stock assessment and marine spatial planning. Also, it increases knowledge on biological interactions and mixing with other stocks and species.

In the final synthesis Chapter 6, the thesis reviews relevant analysis methods of research survey data and underlying data distributions, survey design and stratification, trawl survey inter-calibration and

standardization, as well as estimation procedures and data processing methods in context of the obtained results and methods developed in the thesis. This is done with focus on survey precision and uncertainty (bias, sources of errors) for trawl and acoustic surveys and factors affecting it.

Samenvatting

Bestandsopnames, waarin gegevens worden verzameld over de verspreiding, talrijkheid, biomassa, migratie en biologische parameters van zeevissoorten, vormen een belangrijke pijler onder het visserijonderzoek. Dit proefschrift richt zich op de ontwikkeling en verbetering van onderzoeks-methoden voor de geïntegreerde analyse van verschillende visserij-onafhankelijke bestandsopname technieken (sleepnet, akoestisch, hydrografisch, kieuwnet). In een aantal afzonderlijke deelstudies worden verschillende combinaties van bemonsteringstechnieken geïntegreerd ten behoeve van een verbeterde schatting van de verspreiding en talrijkheid van een vissoort.
Hoofdstuk 2 omvat drie afzonderlijke studies waarin een verbeterde methode om de verspreiding en dichtheidspatronen te schatten met behulp van meerdere technieken. De 1e deelstudie schat de tot nog toe onbekende verspreidings- en dichtheidspatronen van 0-jaar oude kabeljauw in de Oostzee aan de hand van een geïntegreerde analyse van bestandsopnames via sleepnet, hydro-akoestisch onderzoek en hydrografische gegevens. De 2e deelstudie ontwikkelt een nieuwe methode waarbij de correlatie in verspreidings- en dichtheidspatronen in ruimte, tijd, grootte van kabeljauw en wijting worden meegenomen. De nauwkeurigere schattingen dragen bij aan een verbetert inzicht in de relatie tussen jaarklassterkte en paaibiomassa en aan een verbetering van de ‘multi-species’ toestandsbeoordeling in de Oostzee. Daarnaast ondersteunt het een nauwkeuriger zee-beheer en ruimtelijke planning. De 3e deelstudie richt zich op de inter-calibratie van de sleepnetsurvey ter ondersteuning van de internationale ICES BITS bestandsopname. Deze nieuwe methodologie wordt toegepast op Oostzee kabeljauw (en bot).
Hoofdstuk 3 richt zich op verbeteringen in de hydro-akoestische bestandsopname via een verbeterde detectie en bepaling van de lichaamsgrootte en oriëntatie in het water. Deelstudie 4 behandelt de ‘target strength’ van juveniele kabeljauw. Deelstudie 5 presenteert identificatie van rondvissoorten en in het bijzonder jonge kabeljauw. Al deze resultaten dragen bij aan een verbeterde schatting van de verspreiding en talrijkheid van met name jonge kabeljauw.
Hoofdstuk 4 behandelt de schatting van populatie-dynamische parameters. Deelstudie 6 kwantificeert de sterfte, geslachtsrijpheid en groei van kever, een kleine kabeljauwachtige vissoort die een belangrijke rol speelt als prooi voor grotere predatoren, op basis van sleepnet survey informatie, rekening houdend met ruimtelijke variaties. De nauwkeurigere schattingen van deze parameters zijn gebruikt in de toestandsbeoordeling van, en het visserijbeheerplan voor deze vissoort in de Noordzee.
Hoofdstuk 5 richt zich op de integratie van hydro-akoestisch, kieuwnet en hydrografisch onderzoek om de migratiepatronen van pelagische vis te bestuderen. Deelstudie 6 onderzoekt migratie van haring naar paaiplaatsen en voedselgronden in het westelijk deel van de Oostzee. De nauwkeurigere informatie over deze migratiepatronen maakt het mogelijk om een akoestische bestandsopname uit te voeren in verschillende seizoenen. Ook geeft het inzicht in de biologische interacties en de vermenging met andere bestanden.
Hoofdstuk 6 presenteert een synthese van relevante analyse-methodes en onderliggende statistische verdelingen, gericht op de precisie en onzekerheid (bias, fouten bronnen) van bestandsopnames en de factoren die deze beïnvloeden. Hierbij komen de volgende onderwerpen aan bod: ontwerp van de bestandsopname, stratificatie, inter-calibratie en standaardisatie, alsmede ontwerp van de schattings- en dataverwerkingsmethodes.

Appendix A

Appendix A: Definitions and some statistical terms in relation to research survey estimates

Samples are taken to estimate the population, acquired with some measurement error. These are - dependent on the survey design - samples of the true population if the samples are covering the full population. Samples can be either *independent* or *dependent* of each other, i.e. independent or dependent observations. In transects samples may be *serially correlated* (= *auto correlated*).

Precision refers to the way in which repeated observations conform to themselves. A measurement is precise when repeated measurements will yield a very similar result. Precision of the survey estimate of absolute abundance or relative density refers to the size of the deviations from the expected mean obtained by repeated application of the sampling procedures within the same survey (trial), i.e. the precision is the sampling variance of the abundance or density estimate, which is estimated from the within survey variability (Cochran 1977; Godø 1994; Sokal and Rohlf 1997; Beare et al. 2003; Kimura and Somerton 2006). The variance based on the within survey variability often underestimates the actual variance of survey parameters because of changes in survey detection or catch efficiency (catchability) (Pennington and Strømme 1998). There are some a) factors that determine the precision and accuracy (see below) of some survey estimates, and b) some commonly occurring problems and statistical methods in analysing survey data which are described and reviewed in Cochran (1977), Pennington and Strømme (1998) and Kimura and Somerton (2006). Higher precision can be obtained by increasing the number of observations.

Accuracy refers to the closeness between the measurement and the true value. It is possible to measure something very precisely, but arrive at an incorrect value. An accurate measurement is one that is close to the true value. The overall accuracy of the survey can be estimated from the mean squared error (MSE) which is the sum of the sampling variance and the squared bias (Cochran, 1977; Sokal and Rohlf 1997; Kimura and Somerton 2006), where this indicates the range within the estimate would be if the survey was repeated.

True mean is the mean of the population, i.e. the true mean in the sea.

Estimated mean is the mean of the survey estimates which is not always the same as the true mean if the estimate is for example not covering the full population because of the survey design and extension. In surveys, where the distributions are frequently highly skewed, and in which the standard deviation is larger than the mean, there are problems with the sample mean as an estimator of the population mean.

Random errors (or measurement errors) may occur in either direction, but not necessarily equally, and can be reduced by further measurement. Thus these errors can contribute to precision and also to accuracy.

Bias or systematic error goes in one or the other direction (under- or over-estimate), but may not be reduced by increasing the number of measurements or observations. This error does not influence the precision but does influence the accuracy of the observations.

The variance (VAR) of the population is the second moment of a distribution taken about the mean.

The standard deviation (SD) is the dispersion of the population around the mean and equals the square root of the variance. The standard deviation is independent of the number of samples.

The coefficient of variation (Coeff. Var.) is often a more useful measure of dispersion. It is the standard deviation normalized by (i.e. divided by) the mean, and this measure is particularly useful in research and stock surveys where the standard deviation is often related to the mean.

The standard error (SE) is the standard deviation divided by the square root of number of samples, and is accordingly dependent on the number of samples.

The mean squared error (MSE) provides a measure of the total error in an estimate and is the sum of the variance and any biases squared.

Correlation is when densities observed at two nearby points, times or sizes are more likely to be similar than those at positions, times or sizes far apart.

Anisotropic: Autocorrelation in a certain direction (e.g. according to E-W or N-S axis of a transect).

The spatial distribution describes how the fish population varies from one location to the next.

The amplitude distribution of density values describes the different densities that may found in the population. Fish density is a stochastic variable with a statistical distribution where the mean is estimated as the average of a large number of observations.

The *uniform distribution* is when the same amplitude distribution of density values occurs at each point. In a *uniform distribution* the presence of a shoal tends to reduce the likelihood of further shoals. If the spatial stock distribution is non-uniform and that there are regions with high and low density the survey samples may not be independent due to the particular spatial distribution and a sequential sampling method in survey design. The *uniform distribution* can be in form of either a *discrete distribution* or a *continuous distribution*.

A contagiuous distribution is when fish concentrate in certain areas and are scarce in others. If fish have a patchy occurrence, and the local mean density is different in different parts of the area, they show a *contagious distribution*, as opposed to the individual fish being *randomly and independently distributed*.

Over-dispersion can typically be when the distribution of the density observations (catch rates) show a long right tail distribution because fish show aggregating behaviour, i.e. individuals do not behave as independent individuals. Also, there is often correlation between counts in e.g. length groups, and often models which do not include over-dispersion will not adequately describe observations such as the Poisson model for random encounters. The over-dispersion parameter has its basis in the Poisson distribution where it is assumed that variance=mean. In other discrete models as the negative binomial distribution (or in the LGCP model) the variance can be modelled freely so the variance > mean. For the binomial distribution over-dispersion can result in that the more general beta-binomial distribution should be used which allow greater variance than the actual binomial distribution.

The probability Density Function (PDF) is the statistical distribution which controls the individual observations *(to avoid confusion with the spatial distribution which refers to location of fish)*. For *continuous variables* the theoretical probability distribution, or PDF, can be represented by a *continuous curve* (Sokal and Rohlf 1997). For *discrete variables and values* (e.g. fish age or length) the PDF propagate in *discrete countable value jumps* (see also below under *discrete distributions*) The PDF always sums to 1, thus the total area under the PDF is 1. When the fish are *randomly and independently distributed* the PDF is stationary, i.e. same statistical distribution according to time and space. If the fish are in aggregations and are contagious the PDF will be stationary if the aggregations can be found anywhere with equal probability. If the *contagious distribution follows e.g the negative binomial distribution* the presence of a shoal increases the likelihood of another shoal then the shoals can not be found with equal probability and the PDF will be non-stationary. In a *Poisson distribution* the shoals occur randomly anywhere and the PDF will be stationary.

Stationary: In statistics a random variable Y is stationary if all observations of this variable come from the same probability distribution (PDF) independent of time and positions. This is for example that two fish densities at two different stations are drawn from the same statistical distribution. This implies a constant mean abundance over the surveyed area during the survey period. If the statistical distribution changes with time or position it is non-stationary (see above). This type of stationarity is quite distinct from a lack of mobility of fish. Mobile fish concentrations may well have stationary statistical properties.

Continous or discrete distribution: If a random variable is a *continuous variable*, its probability distribution is called a *continuous probability distribution*. A *continuous probability distribution* differs from a *discrete probability distribution* in several ways: a) The probability that a continuous random variable will assume a particular value is zero, b) as a result, a continuous probability distribution cannot be expressed in tabular form, c) but instead, an equation or formula is used to describe a continuous probability distribution (e.g. $y = 1 - 0.5x$). The equation used to describe a continuous probability distribution is called a *probability density function* (PDF). All probability density functions satisfy the following conditions: a) the random variable Y is a function of X and that is $y = f(x)$, b) the value of y is greater than or equal to zero for all values of x, and c) the total area under the curve of the function is equal to 1. The probability that a *continuous random variable* falls in the interval between *a* and *b* is equal to the area under the PDF curve between *a* and *b*.

The normal (or Gaussian) distribtution: In probability theory, the *normal (or Gaussian) distribution* is a very commonly occurring *continous probability distribution or function* - a function that tells the probability that any real observation will fall between any two real limits or real numbers, as the curve approaches zero on either side. Statisticians and mathematicians uniformly use the term normal distribution while physicists sometimes call it a Gaussian distribution because of its curved flaring shape, and also it described as the *bell-shaped curve*. The normal distribution is developed as *an approximation to the binomial distribution*, where the normal distribution is the limiting case of a discrete binomial distribution as the sample size becomes large, i.e. it approximates the exact binomial distribution of events.

The *log-normal (or lognormal) distribution* is in probability theory a *continuous probability distributon* of a random variable whose logarithm is normally distributed. A variable might be modeled as log-normal if it can be thought of as the multiplicative product of many independent random variables each of which is positive.

In mathematics, the *Dirac delta function, or the deltafunction*, is a generalized function, or distribution, on the real number line that is zero everywhere except at zero, with an integral of one over the entire real line. The *delta function* is sometimes thought of as an infinitely high, infinitely thin spike at the origin, with total area one under the spike, and physically represents the density of an idealized point mass. When sample data are positive and right-skewed, the minimum variance unbiased estimator of the mean of the *delta distribution* as a *continuous probability distribution* has been proposed as an appropriate alternative to the sample mean. The estimators are based on the assumptions that the observations can be divided into two groups, zeros and positive values, and that the positive observations are drawn from a lognormal distribution. A *discrete probability distribution* is often represented as a generalized probability density function involving the *delta-functions*, which substantially *unifies the treatment of continuous and discrete distributions*. This is especially useful when dealing with probability *distributions involving both a continuous and a discrete part*.

The *gamma distribution* is in probability theory and statistics a two-parameter family of *continuous probability distributions*. The common *exponential distribution* and *chi-squared distribution* are special cases of the *gamma distribution*.

A *discrete probability distribution* is a *probability distribution* characterized by a probability mass function. The distribution of a random variable is *discrete (dicrete random variable)* when it runs through the set of all possible values and it can assume only a countable finite or countable infinite number of values. The number of potential values needs to be countably infinite even though their probabilities always will sum to 1 (PDF=1), and this requires that the probabilities decline to zero fast enough. Among the most well-known *discrete probability distributions* that are used for statistical modeling are the *Poission distribution*, *the binomial distribution*, and *the negative binomial distribution*. In addition, the *discrete uniform distribution* is commonly used in computer programs that make equal-probability random selections between a number of choices. Equivalently to the above, a *discrete random variable* can be defined as a random variable whose cumulative distribution function increases only by *jump discontnuities* that is, its cumulative distribiution function increases only where it *jumps* to a higher value, and is *constant between those jumps*. The points where jumps occur are precisely the values which the random variable may take.

The *Poisson distribution* is in probability theory and statistics a *discrete probability distribution* that expresses the probability of a given number of events occurring in a fixed interval of time and/or space if these events occur with a known average rate and *independently* of the time since the last event. The *Poisson distribution* can also be used for the number of events in other specified intervals such as distance, area, volume, etc. In a *Poisson distribution* the shoals occur randomly anywhere and the PDF will be stationary.

A *binomial random variable* is the number of successes *x* in *n* repeated trials of a binomial experiment. The *probability distribution of a binomial random variable* is called a *binomial distribution* (also known as a *Bernoulli distribution*).

A *negative binomial random variable* is the number *X* of repeated trials to produce *r* successes in a *negative binomial experiment*. The probability distribution of a negative binomial random variable is called a *negative binomial distribution*. The negative binomial distribution is also known as the *Pascal distribution*. In probability theory and statistics, the *negative binomial distribution* is a *discrete probability distribution* of the number of successes in a sequence of independent and

identically distributed Bernoulli trials before a specified (non-random) number of failures occurs. In the *negative binomial distribution* the presence of a shoal increases the likelihood of another shoal and accordingly the shoals can not be found with equal probability and the PDF will be non-stationary.

(Cochran 1977; Simmonds et al. 1991; Hilborn and Walters 1992; Sokal and Rohlf 1997; Simmonds and MacLennan 2005; Kimura and Somerton 2006; Berg et al. 2014)

Curriculum vitae

Name: J. Rasmus Nielsen
Date of birth: 2nd March 1965
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University education, evaluations, and degrees held
Doctoral candidate defence Wageningen University with defence of approved thesis 26/1-2015 (PhD/Dr.Sc.)...2014-15
Professor qualification evaluation DTU, positive external evaluation 2014
Lecturer MSK Level 4 (Associate Professor, external evaluation) (MSK: With Special Qualifications), DTU.....2010-11
Senior Scientist (external evaluation) DIFRES / DTU Aqua..... 2001
Cand. scient. et mag. art. in Biology and Nordic Philology, University of Copenhagen (KU)..... 1992
Mag. art., Subsidiary Subject in Nordic Philology, KU, (Language, Literature, Communication)..... 1992
Cand. scient. in Biology, KU, specialised in Fisheries Biology and Population Dynamics 1991
Graduate Certificate as Research Fellow in Renewable Resources, MacDonald College, McGill University.....1990
Bachelor in Biology, University of Copenhagen (KU) 1989

Ph.D. and Post Graduate Courses: Doctoral candidate thesis approved for defence 26th Jan. 2015 for the Dutch Doctor of Science degree and subscribed as a doctoral candidate for this degree under Prof. Adriaan D. Rijnsdorp, Inst. Mar. Res. and Ecosystem Studies, Wageningen University (WUR, NL). Possess a long row of graduate and Ph.D. courses from 1990-present at different universities and institutes: Education in University Teaching at DTU (UDTU Courses Modules 1-4) with Diploma (2012-13); Innovation Pedagogics Course DTU (2013); Individual Coaching Course in Research Leadership with Diploma as Head of Research Section (2006); ATLANTIS Ecosystem Model Course (ICES/EU-FP7-Vectors 2011); FLR Modelling and Assessment Courses (ICES, 2007, DTU 2011-2013); GIS Courses (DM 1995, DTU 2007); CTD Hydrographical Course with Diploma (DANA, 1998); Statistical Design Planning Course (DTU 1993); Presentation of Papers in English (DM, 1995); Courses in Assessment Methods (GF-Cph 1988; Nordic Council of Ministers-Nuuk-Greenland 1992); Fisheries Gear Technology Courses (DIFTA 1991, GF-Cph 1991); Fish and Fish Nutrition in Marine Systems (Nordic Council of Ministers Course, Iceland 1989); Graduate Courses in Renewable Resources (as Research Fellow) at MacDonald College, McGill University and Fisheries and Oceans (DFO), Montreal, Canada (1990-91).

Positions held
1. *Research Coordinator and Senior Scientist MSK*, Fisheries Management Division, DTU Aqua…....….2013-
2. *Head of Research Section and Senior Scientist MSK,* Management Systems Section, DTU Aqua ……..2007-2012
3. *Research Coordinator and Senior Scientist,* Fisheries Management Section, DTU Aqua/DIFRES...…...2001-2007
4. *Technical Advisor*, Research Inst. Mar. Products, Vietnam; Danish Government (DANIDA) Project.....1996-1997
5. *Research scientist*, DIFRES, North Sea Centre, Hirtshals and Charlottenlund Castle.....1992-2001
6. *Research scientist*, Greenland Fisheries Research Institute (GF), Copenhagen.....1992
7. *Graduate student employment*, fisheries biology, Greenland Fisheries Research Institute.....1988-1991

Scientific focus and experience
Senior Scientist, Research Coordinator, and Head of Research Section, Fisheries Management and Management Systems, DTU Aqua. He is author of 43 peer reviewed publications (and additionally 12 papers submitted or in submission) and totally of 174 publications. Citations: 400. H-Index: 12 (SCOPUS/Google Scholar); 10 (Web of Science).
He is specialized in fisheries science. His main research is in fish population and fisheries dynamics, stock assessment, and fisheries management and advice including bio-economic fisheries management evaluation tools, fisheries hydroacoustic methods, and research survey design / analysis methods. Important working areas are research in fish stock and fisheries distribution patterns, survey and fish detection methods, fisheries management methods and tools, stock assessment, and research based fisheries management advice. This includes research in main temperate, tropical and arctic marine and fisheries systems (North Sea, Baltic Sea, South China Sea (Vietnam), and North Atlantic (Greenland/Canada) Waters).
He has coordinated (and been initiative taker to) many large international and national research projects, e.g. International Coordinator of EU-FP6-EFIMAS (co-ordinator; www.efimas-project.org), EU-Tender-ISDBITS (coordinator), EU-FP5-EASE (co-coordinator), the International Femern Belt Fish and Fisheries Science Provision Project (coordinator), two Nordic Council of Ministers Research Projects (coordinator), the Sound Bridge Fishery Evaluation Project (coordinator), the national DFFE Herring Selection Project (coordinator), and the DFFE IMPSEL Project. He is national responsible and steering group member of several other international and national research projects incl. task, case study and work package leader (e.g. EU-FP7-BENTHIS, EU-FP7-SOCIOEC, Danish Strategic

Research Council Project IMAGE/MAFIA, EU-FP6-PKFM, EU-FP6-CEVIS, Saudi Arabian Fisheries Science Project, and several EU MARE Tender Projects e.g. Lot2-VMS-Logbook-Coupling, Lot5-Review-BioEconomic-Models, Lot1-EVARES-Survey-Evaluation). He is responsible and initiative taker for research fund raising amounting >130 million DKK (18 million EURO).
He has long international advisory experience; Since 1997 responsible for the ICES WGNSSK North Sea Norway pout stock assessment; co-chair of ICES WGIMM / SGIMM (Integrated Management Modeling, 2011-); alternate national ICES SCICOM Member (2010-); co-chair of ICES IBP Pout (2012); chair of ICES RGANW (2010); chair of ICES AGNOP (2007); and national member of the former ICES Resource Management Committee (RMC, 2006-2010). Appointed to several EU STECF Management Evaluation Working Groups (STECF SGMOS/EWG) and member of other advisory groups (ICES WGBIFS (1999-2004), ICES WGFS (2004-08)). For more than a year scientific advisor in Vietnam, joint Danish Government (DANIDA) & Vietnam Government Development Aid & Research Project. He has produced a long row of advisory notes to national authorities, and has extensive collaboration with national commercial fisheries organizations and international fishery advisory bodies (ICES, NAFO, RACs).
He has been invited co-chair and speaker of Session 7A Ecological-Economic Modelling of the World Fisheries Conference (WFC) Edinburgh Scotland 2012, invited Moderator of Session 507/21B Economic-Ecological Models for EBFM at Conference of the International Institute of Fisheries Economics and Trade (IIFET) Dar-Es-Salaam Tanzania 2012, co-chair of the Session 502 Making Integrated Ecological-Economic Models Useful at Conference of the International Institute of Fisheries Economics and Trade (IIFET) Brisbane Australia 2014, and invited key note speaker at the bi-annual Danish Sea Research Meeting Roskilde January 2013. He is co-chair of and initiative taker to Theme Session M at the ICES Annual Science Conference (ASC), Copenhagen, Sept. 2015.
He has been reviewer of many papers submitted to international well recognized scientific journals and participated in several senior scientist evaluation boards and external PhD project evaluations. He has been supervisor of several PhDs, PostDocs and Master thesis students: Ole Eigaard, PhD (2009-11); Stine D. Ross, PhD, (main supervisor 2011-14); NN, Ph.D (2015-2017; main supervisor, financed by the Saudi Arabian Fisheries Science Project), Francois Bastardie, PostDoc (2007-10), Ole Eigaard, PostDoc (2011-12), Jordan P. Feekings, PostDoc. (50% co-supervisor, 2012-15); Artur Palacz, PostDoc (co-supervisor, 2013-15); Gwladys Lambert, M.Sc. (2007); George Caratzas, M.Sc. (2013); Laurene Pecuchet, M.Sc. (2013). He is university course leader, initiative taker, and responsible for the DTU 25312 Fisheries Systems – Management and Modelling Course, co-responsible and co-course leader for the DTU 25318 Aquatic Ecosystem Management, course leader for a Specialized Course in Marine Spatial Planning, and teacher and module responsible in several other university courses under DTU, KU, RIMP (e.g. the DTU 25307 Fisheries Ecology and Assessment Course, DTU 25309 Design of Surveys and Monitoring Systems Course, 25608 Catch Technology PhD Course). He has been steering Group member of the FAME Research School (FISHNET), and is Advisory Board Member for the IFM institute at Aalborg University. He is international and national Research Project leader, Scientific Expert and Key Consultant and Evaluator for Environmental Impact Assessment and Science Provision Projects to A/S Øresund and A/S Femern Belt under the Danish Ministry of Transport concerning establishment of the Fixed Links in the Sound between DK and S (2003-2008) and in the Femern Belt between DK and D (2009-2014). He is main developer of and reporter to the www.efimas-project.org home page and the associated DocuWiki.

Linguistic skills: Danish and English: Fluently in speech and writing; German and French: Moderate in speech and writing; Norwegian and Swedish: Moderate in speech and writing.

Publications, Totally: 174; Scientific Peer Reviewed Publications: 43; Scientific Peer Reviewed papers submitted, in submission or in advanced prep: 12; Scientific Conference Proceedings, Popular Scientific Publications, and Reports: 119; Additionally a very long row of EU Research Project Deliverables and Interim Reports, ICES Assessment Working Group Reports, ICES Study Group Reports, EU STECF SGMOS & EWG Advisory Reports, DANIDA Project Advisory Reports to the Vietnamese Government an Authorities, and production of many Official Advisory Notes to the Danish Ministry of Food, Agriculture and Fishery.

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4. *Francois Bastardie, F., Nielsen, J.R., Eigaard O., Fock O.H., Jonsson, P., and Bartolino V. 2014.* How spatial planning constrains cross-border fisheries: the bio-economic DISPLACE evaluation on the Baltic Sea. ***ICES J. Mar. Sci. doi:10.1093./icesjms/fsu215, 17 pp.***
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55. *Uzars, D*., Nielsen, J.R.*, Huwer, B.*, and Köster, F.W.* (In Prep).* Feeding Ecology of juvenile Baltic cod according to their distribution and density patterns and habitat affiliation. ***(In Prep.; *Authorship equal)***

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